TOOTH REPLACEMENT IN THE CYNODONT *THRINAXODON LIORHINUS* SEELEY

By

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(With 17 figures in the text)

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Introduction

The very mammalian appearance of the dentition of such theriodont reptiles as the cynodonts invited the assumption that these reptiles replaced their teeth as mammals do and that they had milk and permanent dentitions (Broom, 1913) rather than the indefinite series of replacing teeth occurring in typical reptiles. But Parrington (1936) has shown that in the cynodont *Thrinaxodon* alternately numbered postcanines were replaced at different times. In the eight skulls at his disposal Parrington could show that each of the postcanines was replaced at least once. He divided the material into a younger group in which postcanines nos. 1, 3 and 5 had been replaced shortly before death or were actually undergoing replacement, and an older group in which postcanines 2, 4 and 6 had been replaced shortly before death, and he assumed that the tooth position of the 1st postcanine in the younger group was homologous with the tooth position of the 1st postcanine in the older group. Parrington noted that some of the specimens have six upper postcanines whereas others have seven, but he gave no explanation for this. He claimed that the 7th post-

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canines were unlikely to have had predecessors and were erupting for the first time. Also Parrington described the mandibular postcanines in one specimen in which he noted that the 7th and 8th postcanines had five cusps and the 5th four cusps, instead of the customary three.

Subsequently Brink (1955*b*) has described a very young specimen of *Thrinaxodon*, found in close association with a large specimen which has seven teeth. He formed the opinion that the postcanines were replaced several times during life because the teeth of the young specimen were so much smaller than those of the large specimen. I have (Crompton, 1955) discussed tooth replacement in *Cynognathus* zone and Middle Triassic cynodonts, notably *Scalenodon*. In *Scalenodon* postcanine teeth were found to have been added at the back of the postcanine row during life and a few were lost in front. Fourie (1963) has obtained similar results in *Diademodon*. Recently I (Crompton, 1962) showed that in the bauriamorph *Ericiolacerta* the replacing teeth developed in pits in the alveolar bone lingually to the roots of the functional postcanines and that alternately numbered teeth were replaced at different times.

Material

Four specimens of *Thrinaxodon* have recently been beautifully prepared with the aid of acetic acid by the staff of the British Museum (Natural History). These are B.M.N.H. R3731, R5480, R511a and R511. The first three were studied by Parrington (his specimens E, G and I respectively). I studied three of the British Museum specimens, viz. R3731, R511a and R511. Several specimens in the collections of the South African Museum have also been prepared with the aid of acetic acid. Consequently much additional information on the structure of the tooth crowns and tooth replacement has come to light.

For the purpose of this paper a small skull of *Thrinaxodon* housed in the Universitäts Institut für Paläntologie u. historische Geologie in Munich and the very young specimen of *Thrinaxodon* housed in the Bernard Price Institute for Palaeontological Research in Johannesburg were studied. For convenience the specimens studied have been lettered A to I, as follows:

A = Bernard Price Institute for Palaeontological Research Catalogue No. 274.
B = Universitäts Institut für Paläontologie u. historische Geologie, Munich.
C = B.M.N.H. R3731 = Parrington's Specimen E.
D = S.A.M. K 377.
E = S.A.M. K 380.
F = B.M.N.H. R511.
G = S.A.M. K 378.
H = B.M.N.H. R511a = Parrington's Specimen I.
I = S.A.M. K 379.

The structure of the postcanine teeth indicates that this sample may contain more than one species of *Thrinaxodon*. This is discussed on pp. 511.

Replacement of Individual Teeth

Postcanines: A shallow longitudinal groove (long.g., fig. 2 A and 6 A and D) is present in the maxilla and mandible lingual to the alveolar borders of the postcanines and the canine. This groove presumably housed the dental lamina. Replacement teeth commenced their development in shallow pits (p) in the floor of this groove in the dentary and in the roof of this groove in the maxilla. Initially these pits were separated by a layer of bone from the alveoli of the

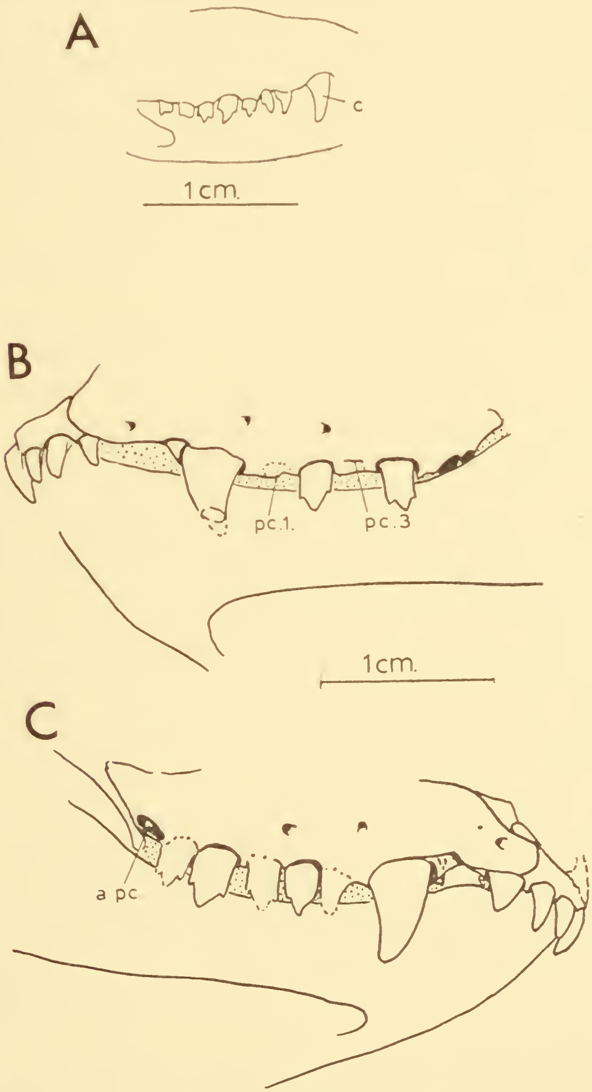


Fig. 1. *Thrinaxodon liorhinus*.
A, right maxillary dentition of Specimen A.
B and C upper dentition of Specimen B.
Key to lettering p. 521.

functional postcanines which lie labial to them. These pits are well preserved in the acid-prepared specimens and in many cases replacing teeth are preserved in the pits (rep.t., fig. 2 B). The functional teeth are usually firmly held in place by a ring of attachment bone around the neck of the tooth. The attachment bone (a.b.) is well preserved around the neck of several postcanines studied and is especially well preserved around the 2nd and 4th upper postcanines of specimen E (fig. 5 A). A ring of small foramina indicates the line of fusion between the attachment bone and the tooth itself. The various stages of the growth of a replacing tooth between its initial development in a pit and its eventual eruption are well shown in the acid-prepared specimens. As the replacing tooth increased in size the pit containing it also increased in size and opened into the alveolus of the functional tooth. The replacing tooth migrated labially and the root of the functional tooth was resorbed to make space for it. Consequently, shortly before the replacing tooth erupted little remained of the root of the functional tooth. At this stage the remaining part of the functional tooth was secured solely by the ring of attachment bone around its neck at the alveolar border. In many specimens the functional tooth was lost at this stage by absorption of the neck of the tooth in a horizontal plane in line with the outer surface of the ring of attachment bone so that nothing visible remains externally to indicate the previous presence of a functional tooth except a ring of foramina in the attachment bone around the remnant of the tooth root. (See fig. 1 B.) This phenomenon accounts for the gaps in the tooth row in the right maxillae of Parrington's specimens A and F. Before the replacing tooth erupted the alveolus was considerably enlarged by the resorption of the attachment bone and the new tooth erupted into an alveolus far larger than the neck of the replacing tooth. Consequently the younger teeth that erupted shortly before death were loosely held in their respective alveoli, e.g. 1st, 3rd, and 5th in the maxilla of specimen C and 3rd, 5th and 7th in the mandible of specimen C (fig. 2). The older teeth, e.g. 2nd and 4th in the maxilla of specimen C (fig. 2 A and B), were firmly held in place by attachment bone.

A replacement cycle identical to that of *Thrinaxodon* appears to have been present in the bauriamorph *Ericiolacerta* (Crompton, 1962) and was also present in *Cistecephalus* zone cynodonts that have been studied by the author.

The material studied for this paper supports Parrington's (1936) conclusion that the odd- and even-numbered postcanines erupted at different times. This is clearly seen in most specimens, e.g. in the maxilla of specimen C (fig. 2 A) the 1st, 3rd and 5th erupted shortly before death and were loosely held in large alveoli whereas the 2nd and 4th were tightly held and have pits for replacing teeth in the maxilla lingual to them. However, it appears that all the odd-numbered (or even-numbered) teeth did not erupt simultaneously; but that the posterior replacing teeth erupted before the anterior teeth of the same set. This is well shown in the right mandible of specimen H (fig. 10 D). The 3rd, 5th and 7th teeth are loosely held in the alveoli and erupted shortly before death. The 7th tooth was fully erupted, the 5th partially erupted and the 3rd was still completely contained in its alveolus. In terms of alternate replacement a replacing tooth would be expected to be present in the first alveolus. However, the old functional tooth is still present in this position, but a deep pit for a well-developed replacing tooth is present adjacent to the old 1st functional postcanine. In the left mandible (fig. 10 C) the condition is similar to that in the right, except that the old functional 1st postcanine has been lost and a partially displaced replacing tooth is present in the first alveolus. This evidence suggests that the odd-numbered replacing postcanines erupted in the following order: 7th, 5th, 3rd, 1st. In the maxilla of specimen F (fig. 6 A) the replacing tooth for the 6th postcanine (r.pc.6.) is larger than that for the 2nd (r.pc.2.) and that of the 4th is intermediate in size between the 2nd and the 6th. The younger postcanines, i.e. 1st, 3rd and 5th of this maxilla, that are loosely held in their alveoli appear to have erupted in the following order: 5th, 3rd, 1st. A similar phenomenon can be observed in most of the specimens studied with the exception of the lower postcanines of specimen G (fig. 9) where the rule of alternate replacement seems to break down over a short distance.

In most reptiles that actively replace their teeth a wave of replacement passes along each alternately numbered tooth series either from back to front or front to back (Edmund, 1960, 1962). In *Thrinaxodon* the wave passes from back to front.

Canines: Replacing canines are present in both the upper and lower jaws of most specimens of *Thrinaxodon* studied. The replacing canines commenced their replacement in distinct pits in the maxilla and dentary. In the specimens studied the pits in the maxilla (specimen E, fig. 5 A) are always found antero-lingual of the functional canine whereas the pits in the dentary (specimen E, fig. 5 B) are always found postero-lingual of the functional tooth. As the replacing canine enlarged, the pit containing it fused with the main alveolus (specimen D, fig. 3 A and B) and the replacing canine migrated to lie in front of the functional canine in the upper jaw and behind the functional canine in the lower jaw (specimen F, fig. 6 B and D). Fourie, however (1963), has described a specimen of *Thrinaxodon* in which the upper replacing canine lies behind the functional canine.

Incisors: The incisor region is not well preserved in most of the specimens studied. The replacing incisors appear to have developed in pits behind the functional ones. These pits, where preserved, are confluent with the alveoli of the functional teeth. In the premaxilla of specimen F (fig. 6 A and B) replacing teeth are present behind all four incisors. It is not possible to determine the order of replacement of the functional incisors.

Structure of the Crowns of the Postcanines

In a few instances Parrington (1936) was able to describe additional cusps on the lingual side of the crowns of upper postcanines. In the acid-prepared specimens the whole structure of the crowns of the teeth can be studied, and it

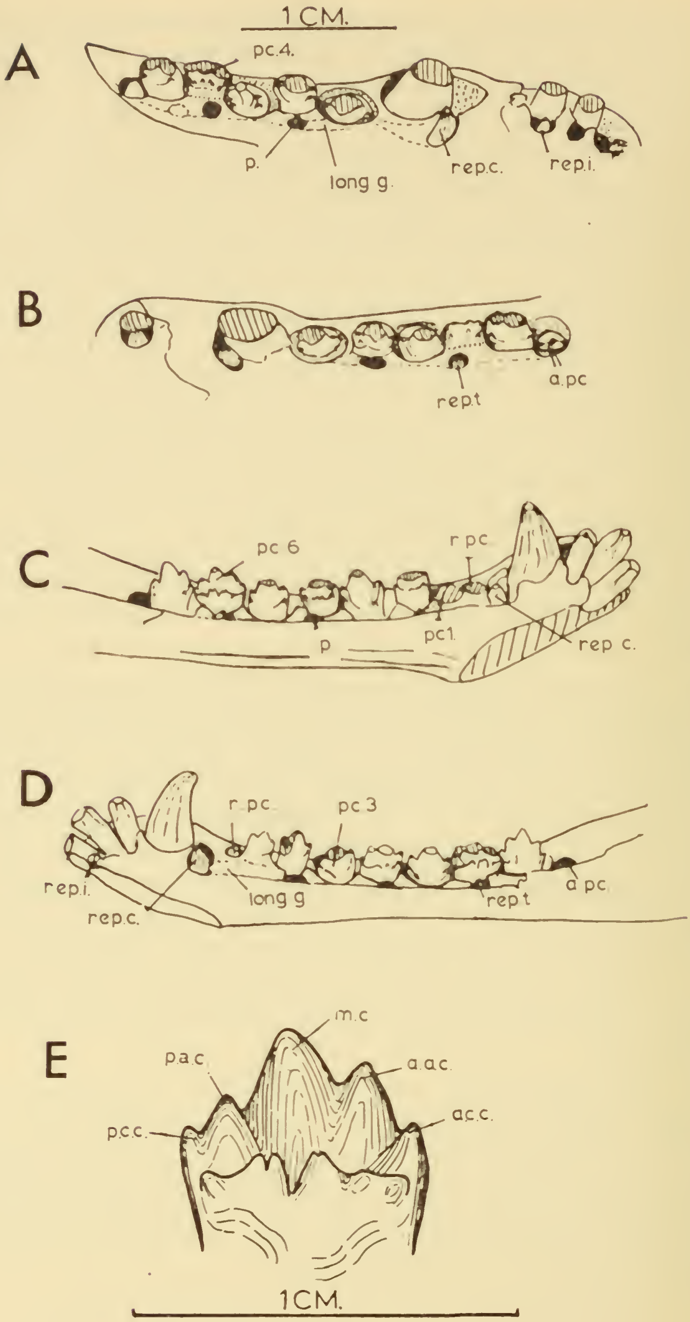


Fig. 2. *Thrinaxodon liorhinus*, Specimen C.
A and B upper dentition, C and D, lower dentition and
E, lingual view of the lower 6th postcanine.
Key to lettering p. 521.

has been found that in many cases quite complex patterns are present which differ considerably from the simple crown pattern usually associated with *Thrinaxodon*.

On the basis of the pattern of the crowns of the lower posterior postcanines, it is possible to divide the specimens studied into three ill-defined groups. Specimens A, B or I, however, cannot be assigned to any of these groups as the structure of their lower postcanines is not known. The members of the three groups form a consecutive series of increasing size (see table I, page 500).

Group I consists only of specimen C.

Group II consists of specimens D, E, F and G.

Group III consists of specimen H.

Group I

Lower Postcanines. Specimen C (fig. 2 C, D and E)

Seven lower functional postcanines are present. A remnant of a tooth (r.pc.) is present anterior to the 1st functional postcanine and an unerupted postcanine (a.pc.) which does not appear to have had a predecessor is present behind the last functional postcanine.

The crown structure of the more recently erupted 3rd, 5th and 7th postcanines is different from that of the older 2nd, 4th and 6th. In each series, i.e. the odd-numbered, 3rd, 5th, 7th and the even-numbered 2nd, 4th and 6th, the crown pattern becomes increasingly complex in a posterior direction. Of great interest and importance is the fact that each of the more recently erupted teeth has crowns with a simpler pattern than the older teeth anterior or posterior to it. The tooth with the most complex crown is the 6th postcanine (fig. 2 E). It consists of three cusps aligned antero-posteriorly; a main cusp (m.c.), an anterior accessory cusp (a.a.c.) and a posterior accessory cusp (p.a.c.). Because the anterior accessory cusp is larger than the posterior accessory cusp the anterior margin of the main cusp is shorter than its posterior margin. Anterior to the anterior accessory cusp and posterior to the posterior accessory cusp two smaller cusps are present. These have for convenience been designated as anterior and posterior cingular cusps (a.c.c., p.c.c.) respectively. It is, however, extremely difficult to determine whether the anterior and posterior cingular cusps do in fact develop upon a definite cingulum. In some cases this appears to be the case, but in other cases these cusps appear to be quite distinct from the cingulum. A well-developed cingulum is present on the lingual surface of the crown. It supports a series of small cusps. The largest are twin cusps that lie either side of the midline. A deep valley separates the anterior and posterior twin cusps. Two small cuspules are present anterior to the twin cusps and one is present posterior to them.

The crown pattern of the 4th and 2nd postcanines is similar to that of the 6th except that accessory and the anterior and posterior cingular cusps and the cusps on the lingual cingulum are not so well developed. The crowns of the younger 7th, 5th and 3rd postcanines in the odd-numbered series also consist of three cusps (anterior accessory, main and posterior accessory) aligned antero-posteriorly. The anterior and posterior cingular cusps are situated low down on the lingual surface of the anterior and posterior accessory cusps and they do not lie anterior or posterior to the latter as they do in the 6th postcanine. In the odd-numbered teeth no cusps appear to be present on the lingual side between the anterior and posterior cingular cusps.

Upper postcanines (fig. 2 A and B)

As in the lower postcanines there is a great difference between the older and younger postcanines, but this is not as marked as in the lower jaw. The crowns are in many cases damaged.

Six functional postcanines are present. The even-numbered erupted later than the odd-numbered. The 6th postcanine has apparently been shed and an unerupted postcanine is visible above it. The crown of the 4th postcanine, which is a member of the older series of teeth, consists of three antero-posteriorly aligned cusps, anterior and posterior cingular cusps and a series of cusps upon a lingual cingulum. The cingulum of the crown of the second postcanine is very poorly developed and supports only an anterior cingular cusp. In the younger 5th and 3rd postcanines anterior and posterior cingular cusps are present but no cusps are present on the lingual cingulum.

Group II

Lower postcanines. Specimen D (fig. 3 B and C and 4B)

Seven functional postcanines are present. A remnant of a tooth root (r.p.c.) is present anterior to the 1st. A small, apparently non-functional tooth is present behind the 7th postcanine (pc.8.). This tooth is completely covered laterally by the anterior border of the coronoid process. As in specimen C, the crowns of the older teeth are different from those of the younger teeth.

The sixth postcanine (fig. 4 B), belonging to the older series, has three cusps (anterior accessory, main and posterior accessory) aligned antero-posteriorly. The main cusp and the anterior accessory cusp are about the same size and the posterior accessory is slightly smaller. The posterior cingular cusp lies directly behind the posterior accessory cusp whereas the anterior cingular cusp lies slightly antero-lingually of the anterior accessory cusp. As a result the crown, when viewed from above, has a wide, blunt anterior region and a tapering posterior region. A large and prominent cingular cusp (c.c.) is present on the lingual surface below the junction of the main and anterior accessory cusps. A small poorly defined cuspule is present posterior to this cusp. A poorly developed cingulum (cing.) is present between the two lingual cingular cusps (c.c.) and the posterior cingular cusp. In the fourth postcanine the main cusp is considerably larger than the accessory cusps. The anterior cingular cusp is fairly well developed, but the posterior cingular cusp is small and the cingulum and cusps upon the cingulum are very poorly developed. When viewed from above, the crown has a wide anterior region and a tapering posterior region, as in the 6th postcanine. The 4th postcanine is shorter but wider than the 6th.

In the second postcanine the crown is dominated by the main cusp and the anterior and posterior accessory cusps and the anterior and posterior

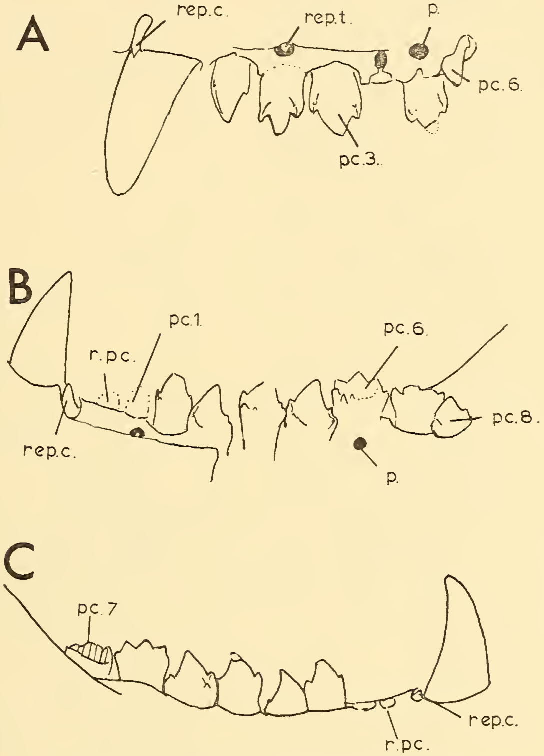
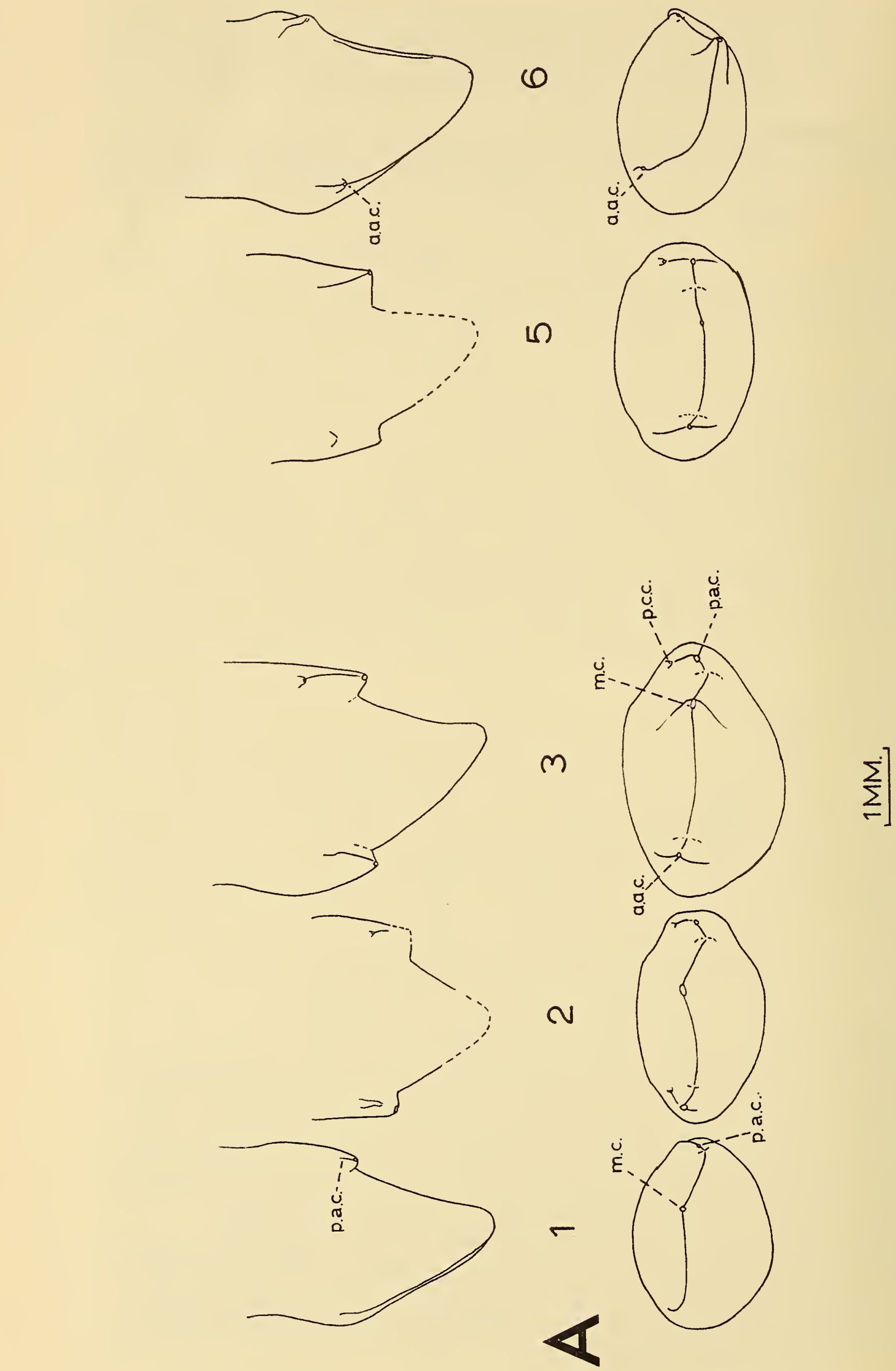


FIG. 3. *Thrinaxodon liorhinus*, Specimen D.
A, lingual view of the upper postcanines,
B, lingual and C, labial view of the lower postcanines.
Key to lettering p. 521.

cingular cusps are very small. The lingual cingulum is absent. In crown view the tooth is more circular than the 4th postcanine. Within the even-numbered postcanines there is, therefore, in a posterior direction a progressive increase in the size of the accessory and cingular cusps and a progressive decrease in the size of the main cusp relative to the size of the accessory cusps. In addition posteriorly the teeth become progressively more longitudinally ovate.

Similar tendencies can be observed in the odd-numbered teeth of the same specimen, but the structure of the crown is slightly different. Unfortunately the crown of the 7th postcanine is partially destroyed. The remaining portion is similar to the 5th except that the cingulum and cingular cusps are absent and it is more longitudinally ovate.


A
1
2
3
5
6
p.a.c.
m.c.
a.a.c.
p.c.c.
1MM.

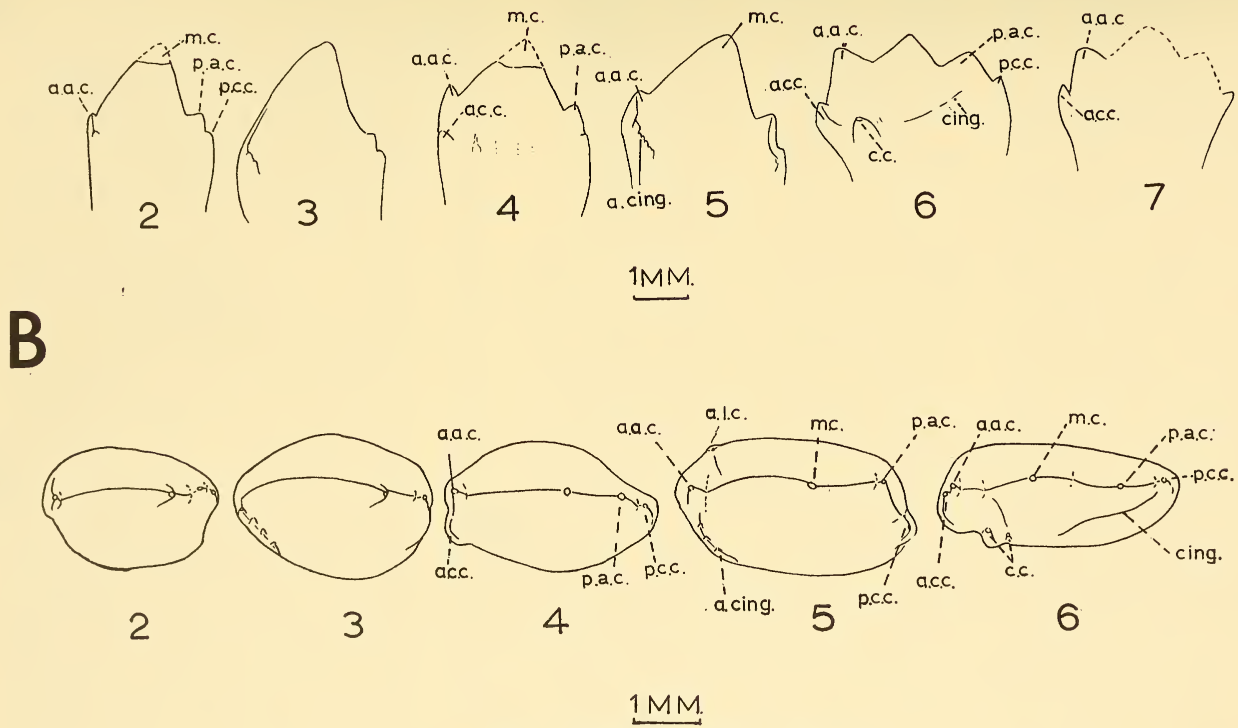


FIG. 4. *Thrinaxodon liorhinus*, Specimen D.
A, lingual and crown views of the upper postcanines and
B, lingual and crown views of the upper postcanines.
Key to lettering p. 521.

In the 5th postcanine the crown is dominated by the main cusp and the accessory cusps are small. In contrast to the even-numbered teeth the posterior cingular cusp does not lie directly behind the posterior accessory cusp, but postero-lingually to it. A well-defined anterior cingular cusp is absent; in its place is a series of small cuspules arranged to form a short ridge (a.cing.) running downwards in a posterior direction. Because the posterior cingular cusp is well developed and the anterior cingular cusp poorly developed, the crown has a wide (transverse) posterior region and a slightly tapered anterior region, i.e. opposite to the conditions in the even-numbered teeth. A small cuspule (a.l.c.) called the anterior labial cusp is present on the labial surface of the tooth below the junction of the main and anterior accessory cusps. The 3rd postcanine is similar to the 5th except that the main cusp is relatively larger and the remaining cusps relatively smaller. The cuspule on the labial surface is absent.

It is clear from the above description that the crowns of the odd-numbered series (3, 5 and 7) have the same basic structure and that this is quite distinct from the structure of the crowns of the even-numbered series (2, 4 and 6). In each series, however, the teeth become more complex in a posterior direction. Thus not only do the odd- and even-numbered teeth replace at different times in specimen C, but in addition the crown patterns of the two series are distinct from one another.

The 8th postcanine is an enigma. It is smaller than any of the other lower postcanines with the exception of the first. The main cusp dominates the crown. The only part of the cingulum developed is the anterior cingular cusp. It is discussed on p. 509. The last upper postcanine of this specimen is also of a simpler construction than the penultimate tooth. This is the only specimen in the series in which this phenomenon was observed.

Specimen E (fig. 5 B, C, D)

This specimen is larger than D, but the individual teeth are smaller than those of D.

Seven functional lower postcanines are present. The remnant (r.pc.) of a tooth is present anterior to the 1st postcanine. Partially erupted 8th postcanines were present on both sides, but have been lost from the specimen. These teeth appeared to have had no functional predecessor as there are no indications of a root remnant in their alveoli. Unfortunately only the 6th and 7th postcanines are well preserved. The crowns (fig. 5 C and D) of these two teeth are characterized by a mixture of the features present on the crowns of the 6th and 7th postcanines of specimen D. In both, the accessory cusps are nearly as large as the main cusps. In the 6th postcanine the anterior cingular cusp lies almost directly in front of the anterior accessory cusp, but the posterior cingular cusp lies slightly postero-lingually to the posterior accessory cusp. Two well-developed cingular cusps (c.c.) are present on the lingual surface at the base of the anterior accessory cusp. These are followed posteriorly by three

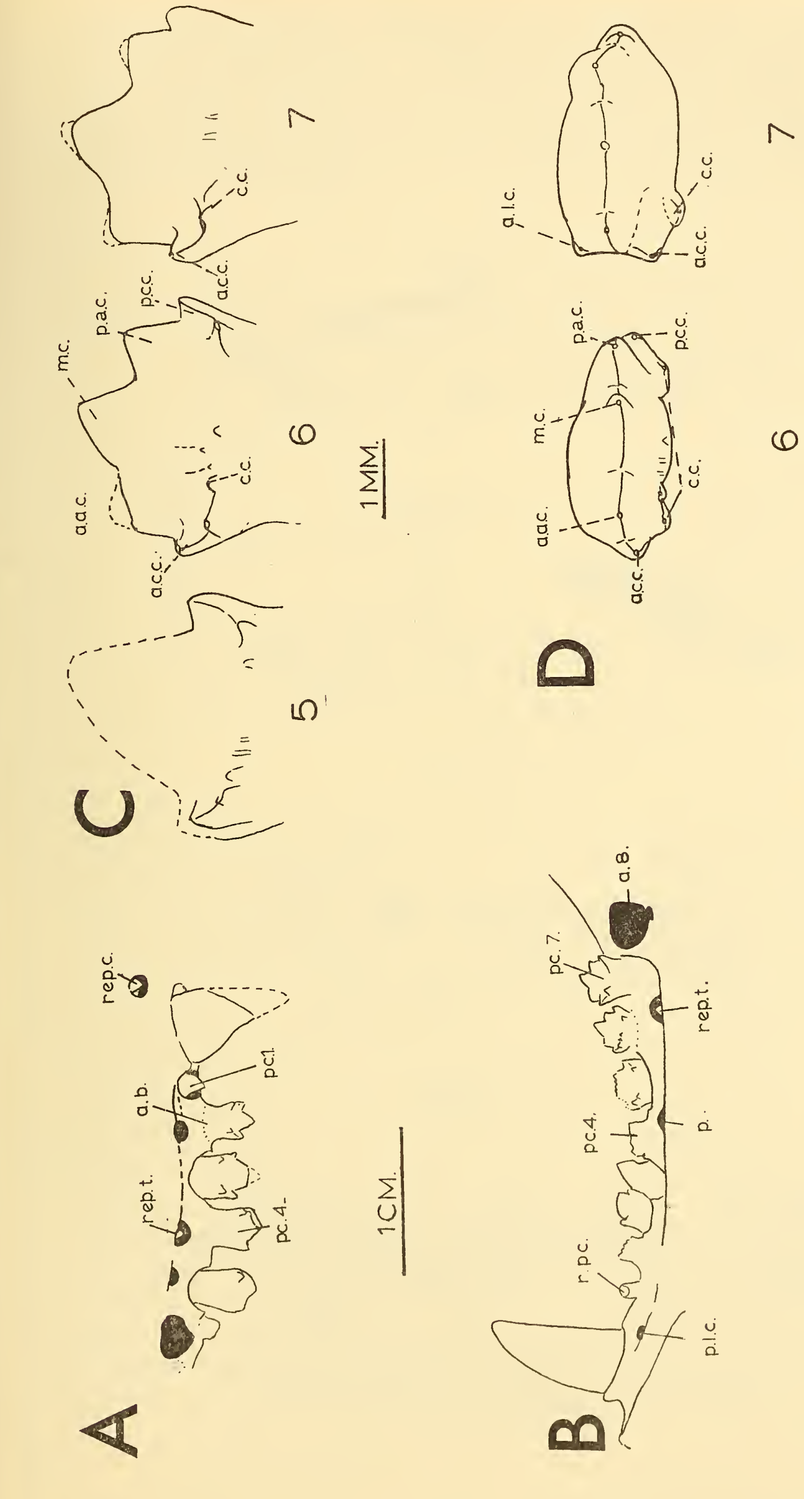


FIG. 5. *Thrinaxodon* sp., Specimen E.

A, lingual view of the upper postcanines;
B, lingual view of the lower postcanines;
C, lingual view of the 5th, 6th and 7th postcanines;
crown view of the 6th and 7th postcanines.

Key to lettering p. 521.

minute cuspules. A well-developed cusp is present on the lingual surface of the base of the posterior cingular cusp. This tooth is almost identical with the 6th postcanine of specimen D. In the 7th postcanine the anterior cingular cusp is presumably represented by a well-developed cusp antero-lingual to the anterior accessory cusp. A single large cingular cusp (c.c.) is present below the junction of the anterior cingular cusp and anterior accessory cusp. No further cusps are

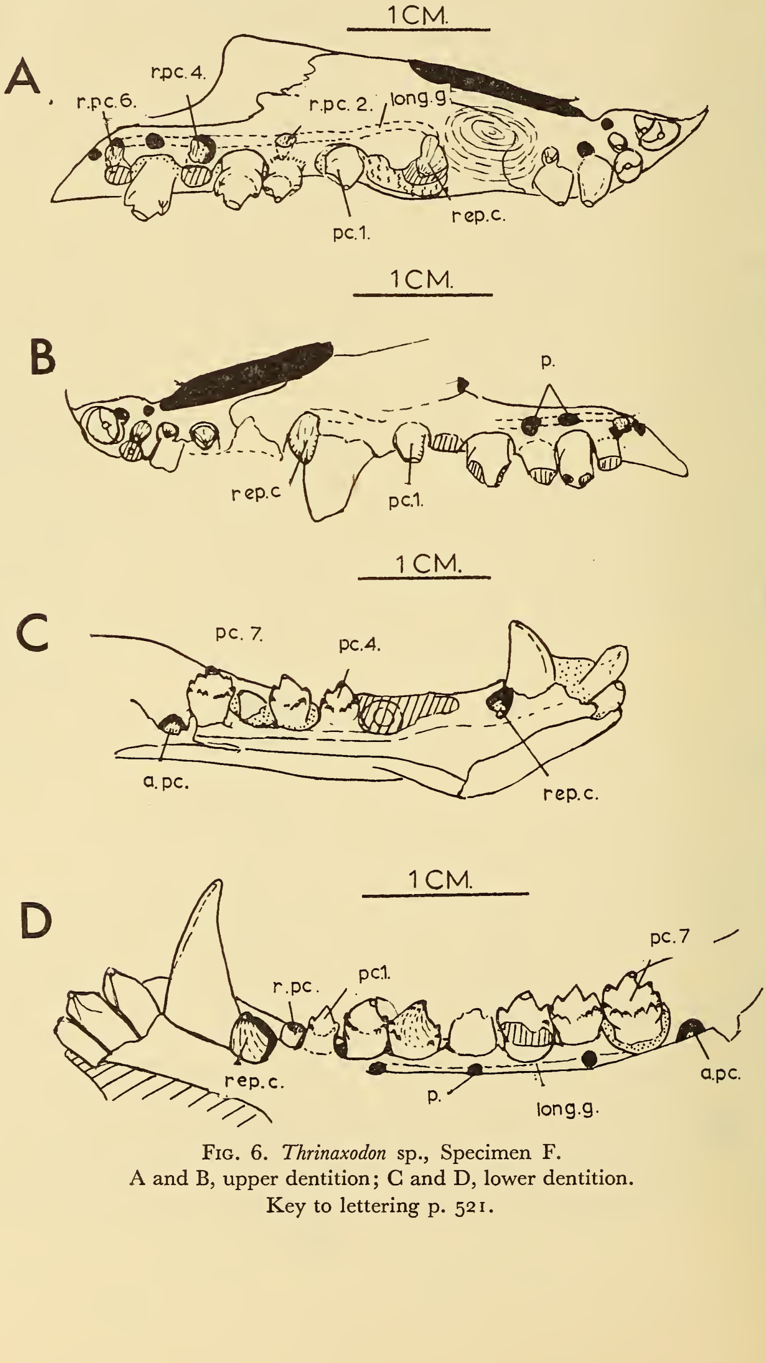


Fig. 6. *Thrinaxodon* sp., Specimen F.
A and B, upper dentition; C and D, lower dentition.
Key to lettering p. 521.

present behind this cusp between it and the posterior cingular cusp. A well-developed cusp is present on the labial surface (a.l.c.) antero-labial to the apex of the anterior accessory cusp when seen in crown view. The 5th postcanine apparently had a high dominant main cusp. The anterior cingular cusps are arranged to form a ridge not unlike a similar structure of the 3rd and 5th postcanine of specimen D.

Specimen F (Fig. 6 C and D and fig. 7)

The lower postcanines of specimens F and G are more similar to one another than they are to those of specimens D and E, but because of numerous similarities all four specimens have been placed in Group II.

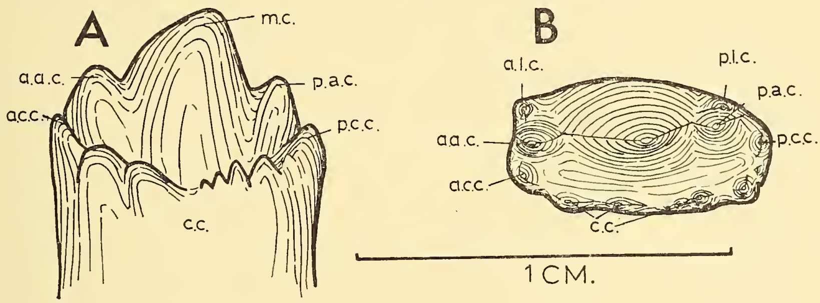


FIG. 7. *Thrinaxodon* sp., Specimen F.
A and B, lingual and crown views of the 7th lower postcanine.
Key to lettering p. 521.

Seven functional postcanines are present in the right mandible (fig. 6 D). They are preceded by the remnant of a tooth (r.p.c.) and an unerupted and partially formed tooth (a.p.c.) is present in a crypt behind the last postcanine. The crowns of the individual postcanines are not sufficiently well preserved to permit a detailed comparison of the crown structures of odd and even postcanines, but the differences do not appear to be as marked as in specimens C and D. As in other specimens there is a progressive complication of the crowns in a posterior direction. The crowns are characterized by well-developed cingular cusps. These are particularly well preserved in the 7th functional postcanine (fig. 7). In this tooth the accessory cusps are large (a.a.c., p.a.c.), but not as large as the main cusp. An anterior cingular cusp is present antero-lingual to the anterior accessory cusp. It is followed by two large cingular cusps (c.c.). The posterior portion of the cingulum consists of a series of six cuspules which, with the exception of one, increase progressively in size in a posterior direction. Well-developed cuspules are present on the labial surface of the crown at the base of the anterior and posterior accessory cusps (a.l.c., p.l.c.). With the exception of the cusps on the posterior portion of the cingulum this tooth is almost identical to the 7th postcanine of specimen E (fig. 5 C and D).

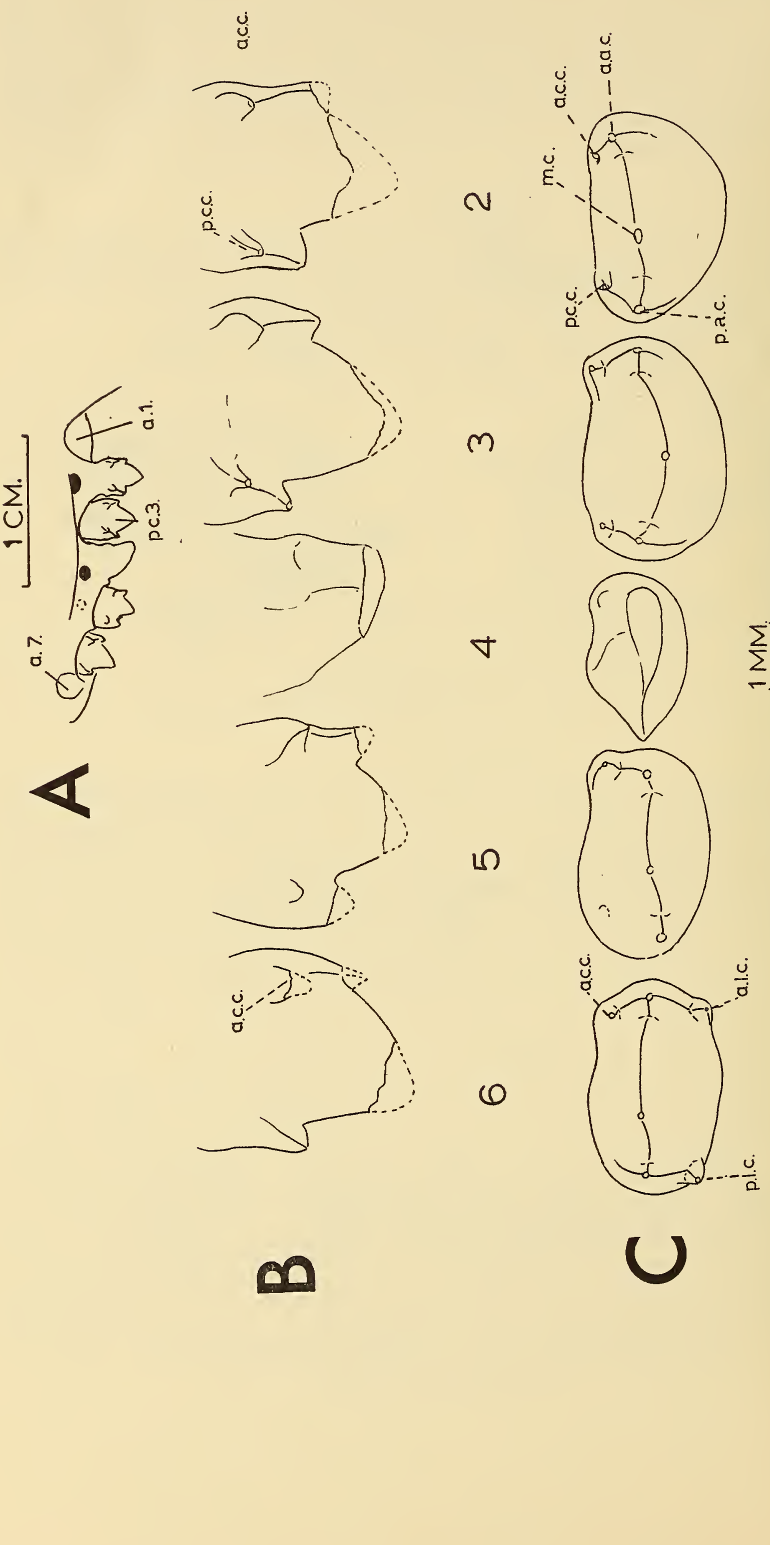


Fig. 8. *Thrinaxodon* sp., Specimen G.

A, lingual view of the upper postcanines;
B, lingual and C, crown views of the upper postcanines.

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Specimen G (fig. 9)

The jaw contains eight functional postcanines. The 8th, 5th and 3rd appear to have erupted shortly before death. The 6th tooth is missing. The remaining teeth are all badly worn. This is the only specimen in which postcanines show advanced signs of wear and in which replacement does not appear to be strictly alternate.

The crown of the 5th postcanine (fig. 9 B and C) is almost identical to the 7th functional postcanine of specimen F (fig. 7) except that the posterior cingular cusp (p.c.c.) lies lingual to and not posterior to the posterior accessory cusp. The 8th postcanine of specimen G is identical to the 5th except that it lacks the posterior labial cusp and is more longitudinally ovate. The anterior part of the cingulum of the 3rd postcanine does not support the three large cusps that are present in this position in the 5th and 8th postcanine, but consists of a series of six small cusps arranged to form a ridge which terminates anteriorly at the base of the anterior accessory cusp. The posterior cingulum supports a single well-developed cusp (p.c.c.) postero-lingual to the posterior accessory cusp. This tooth is similar to the 5th functional postcanine of specimen D (fig. 4 B). In postcanines nos. 8, 5 and 3 the main cusp becomes progressively larger in an anterior direction and the accessory cusp progressively smaller. The 2nd and 4th postcanines although badly worn are characterized by large anterior cingular cusps and poorly developed posterior cingular cusps. In this respect they are not unlike the 6th postcanines of specimen D (fig. 4 B) and Specimen E.

Upper postcanines, *Specimen D* (figs. 3 A and 4 A)

Without exception the upper postcanines have crown patterns less complex than those of the corresponding lower teeth. Six functional postcanines are present in specimen D. The 6th is preserved partially erupted. The 1st and 3rd appear to have erupted shortly before death. The 5th already has a large pit for a replacing tooth at its base. The 1st postcanine (fig. 4 A) consists of a large main cusp, which is slightly recurved; the anterior accessory cusp is missing, but a small posterior accessory cusp (p.a.c.) is present. A cingulum and cingular cusps are absent. The 3rd postcanine has a large main cusp which is flanked by smaller anterior and posterior acccssory cusps. A small posterior cingular cusp is present on the lingual surface at the base of the anterior accessory cusp. No other cingular cusps are present. The 5th postcanine is similar. The 6th postcanine is almost identical to the 1st postcanine except that it possesses a very small anterior accessory cusp. The 2nd postcanine appears to have both anterior and posterior cingular cusps.

Specimen E (fig. 5 A)

Six functional postcanines are present. The 1st, 3rd and 5th are only partly erupted indicating that they erupted shortly before death. The structure of the crowns of the postcanine teeth are identical to those of specimen D.

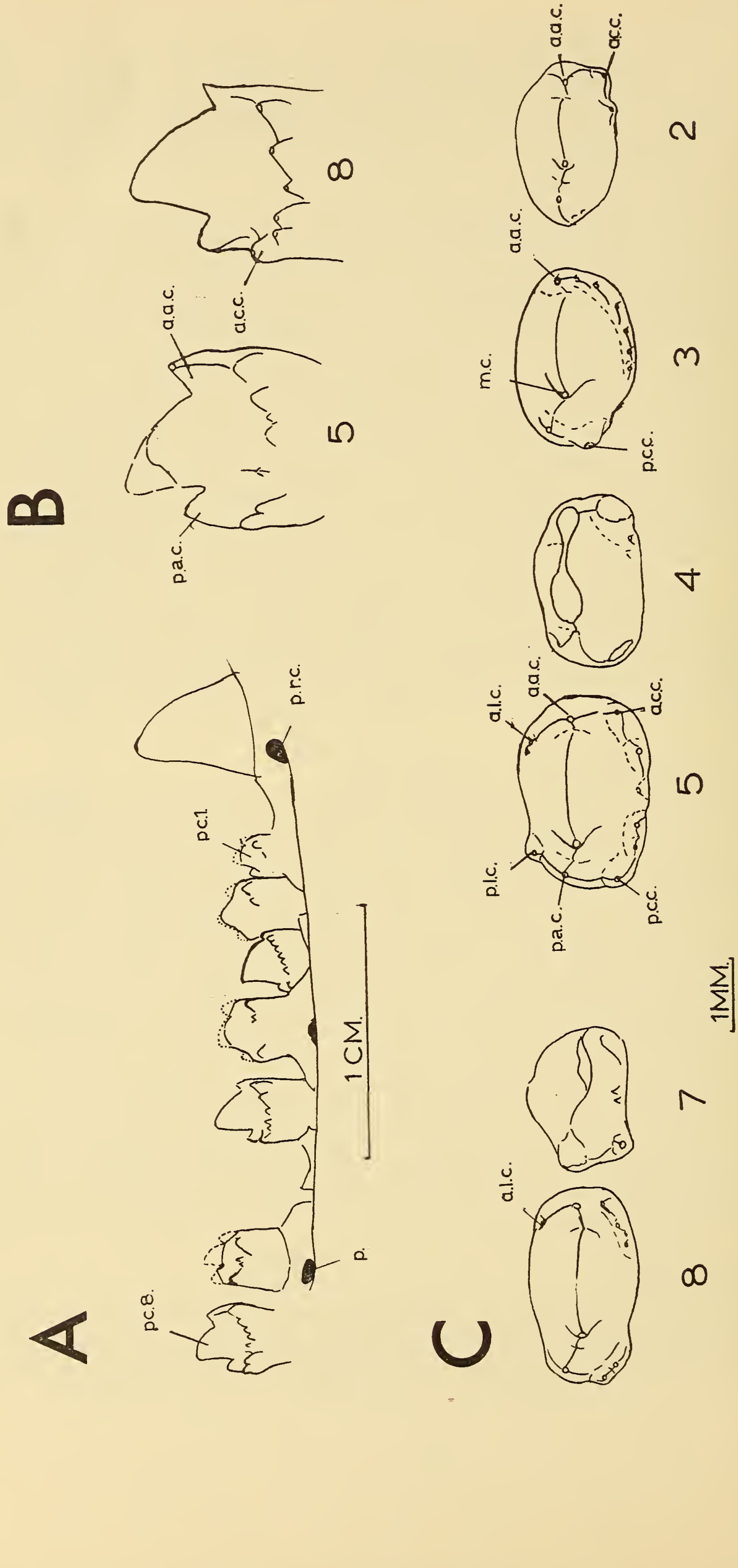


FIG. 9. *Thrinaxodon* sp., Specimen G.
A, lingual view of the lower postcanines;
B, lingual view of the 5th and 8th postcanines;
C, crown views of the 2nd to 8th postcanines.
Key to lettering p. 521.

Specimen F (fig. 6 A and B)

Six functional postcanines are present in specimen F. The 1st, 3rd and 5th erupted shortly before death and well-developed replacing teeth are present in pits at the bases of the older 2nd, 4th and 6th postcanines. The crypt for an additional tooth is present behind the 6th postcanine. The structure of the crowns of the upper postcanines is identical to those of specimens D and E.

Specimen G (fig. 8)

Six functional teeth are present. In the even-numbered series the 2nd and 4th have well-developed pits for replacing teeth above them, but the replacing tooth for the 6th had already erupted before death. The 2nd and 3rd teeth are almost identical in structure and possess well-developed anterior and posterior cingular cusps. The 4th is badly worn. The 5th and 6th lack well-developed posterior cingular cusps. The 6th has two well-developed cusps on the labial side of the tooth (p.l.c., a.l.c.) one above the anterior and one above the posterior accessory cusp.

Group III

Lower postcanines. Specimen H (fig. 10 C and D)

The lower postcanines of this specimen are characterized by poor development of the cingulum and cingular cusps. In this respect they are quite different from the lower postcanines of Groups I and II. The lower postcanines of specimen H closely resemble the upper postcanines of this and other specimens. Seven functional postcanines are present. The crown of the 7th consists of the characteristic main cusp, anterior and posterior accessory cusps, and anterior and posterior cingular cusps. In the 5th and 3rd the crown structure is similar except that the main cusp becomes progressively more dominant in an anterior direction.

Upper postcanines. Specimen H (fig. 10 A and B)

Six functional postcanines are present in the right maxilla. The cingular cusps are very poorly developed and appear to be entirely absent on most of the postcanines.

Discussion

Extension of Growth series of 'Thrinaxodon'

The present study has confirmed Parrington's (1936) conclusion that alternate replacement took place in the postcanine teeth of *Thrinaxodon*. Parrington showed that it was possible to divide the specimens of *Thrinaxodon* that he studied into two groups; a younger group in which the 1st, 3rd and 5th maxillary postcanines were younger than the remaining ones and an older group in which the 2nd, 4th and 6th maxillary postcanines were younger than the others.

The skull lengths of Parrington's younger group vary between 61 mm. and 79 mm. (see table I). One of Parrington's specimens, viz. his E (C in the present investigation), was prepared in acid and it has been confirmed that the 1st, 3rd and 5th maxillary postcanines were the younger. Four additional skulls falling within this size range were studied. These are specimens D, E, F and G. In all of them the 1st, 3rd and 5th postcanines were the younger. The skull lengths of these specimens are given in table I. Parrington concluded that the 1st, 3rd and 5th teeth were replaced at least once and that the 2nd,

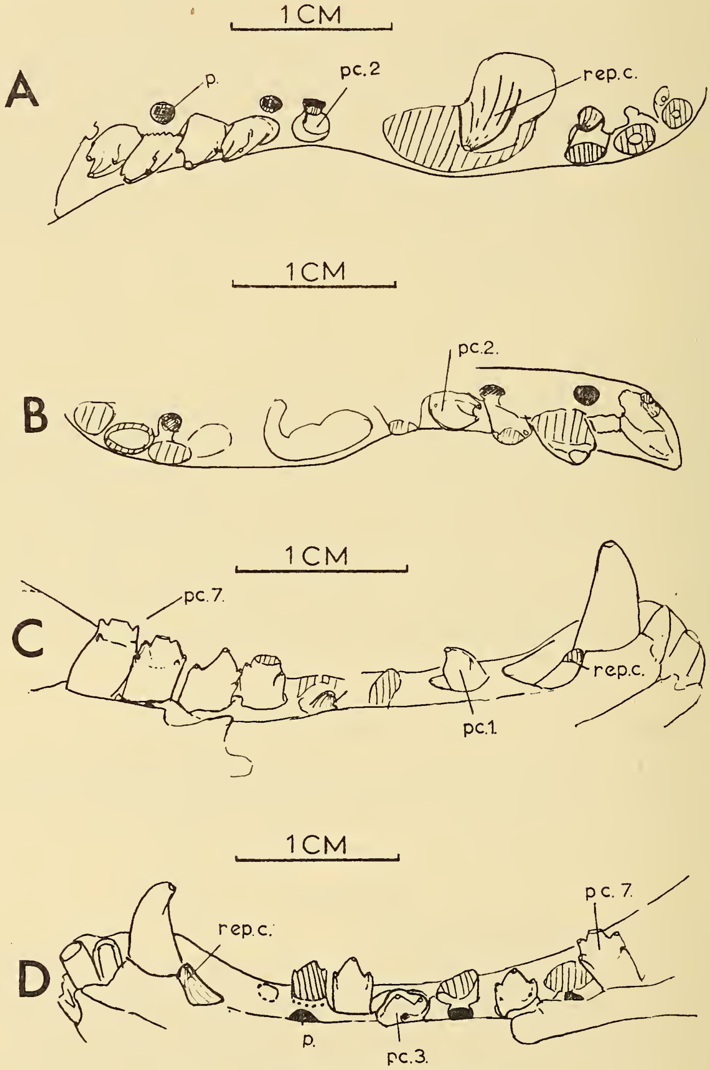


Fig. 10. *Thrinaxodon* sp., Specimen H.
A and B, upper and C and D, lower dentitions.
Key to lettering p. 521.

4th and 6th were also replaced at least once. Parrington's two stages are diagrammatically shown in figure 11 A. In this figure they are labelled II and III. Fully erupted teeth are drawn in black below the alveolar border and unerupted replacing teeth in dotted lines above the alveolar border. Only the portion below the alveolar border of partially erupted teeth is shown in black.

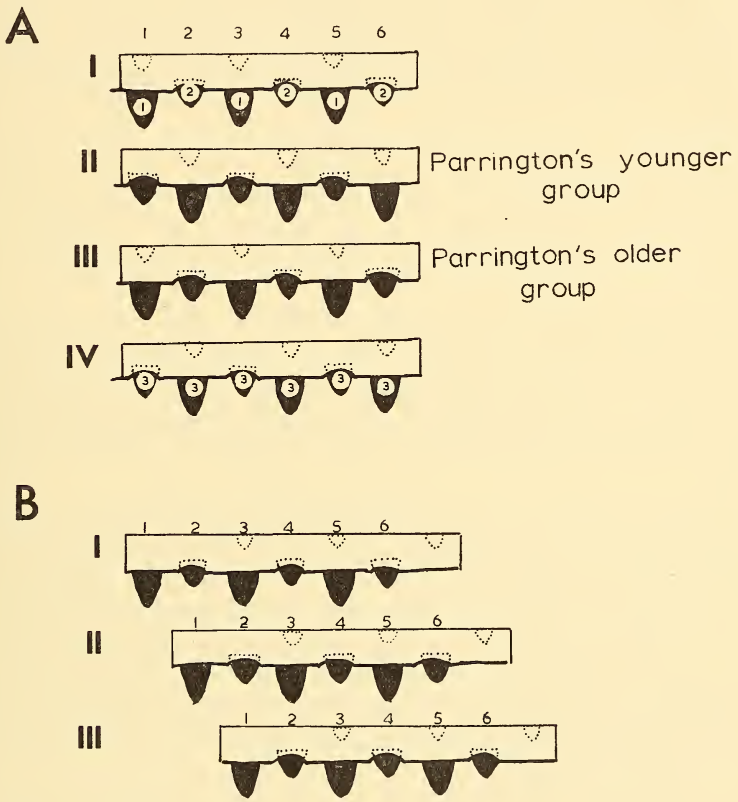


FIG. 11. Tooth replacement in *Thrinaxodon.*

A, diagram to illustrate simple alternate replacement concluded by Parrington to have been present in *Thrinaxodon.* Additional growth stages I and IV have been added.

B, diagram to illustrate a possible way in which posterior migration of the post-canine row could have been achieved.

In figure 11 A, stage II, the 1st, 3rd and 5th are partially erupted and in figure 11 A, stage III, the 2nd, 4th and 6th of stage II have been replaced and partially erupted teeth are present in these alveoli. Specimens both larger and smaller than those available to Parrington were available for the present study. See table I.

TABLE I

Designation of specimens in present paper	*Designation of specimens in Parrington's* (1936) *paper*	*Length of skull* (*tip of snout to posterior end of sagittal crest*)	*Youngest teeth*						
			1	2	3	4	5	6	7
A		36 mm.		×		×		×	
B		58 mm.		×		×		×	
	B	61 mm.	×		×		×		
	C	63 mm.	×		×		×		
C	E	68 mm.	×		×		×		
	F	70 mm.	×		×		×		
D		73 mm.	×		×		×		
E		78 mm.	×		×		×		
	G	78 mm.	×		×		×		
F		78 mm.	×		×		×		
G		80 mm.	×		×		×		
	H	82 mm.		×		×		×	
H	I	85 mm.		×		×		×	
I		86 mm.	×		×		×		

In specimen A (fig. 1 A) the 2nd, 4th and 6th postcanines were younger than the 1st, 3rd and 5th. This skull is incomplete, but as reconstructed by Brink (1955*b*) it could not have had a skull length of much more than 36 mm. It is the youngest specimen available and in comparison with older specimens the teeth are minute. It has seven functional postcanines. This fact is discussed on p. 502.

In specimen B (fig. 1 A and B) (skull length 58 mm.) the 2nd, 4th and 6th postcanines were also the youngest. The difference in the size of the corresponding teeth in A and B suggests that several growth stages intervened between specimens A and B. In specimens with skull lengths between 61 mm. and 80 mm. the 1st, 3rd and 5th teeth were the younger. From 80 mm. to 85 mm. the 2nd, 4th and 6th were the younger. In a damaged *Thrinaxodon* skull (referred to as specimen I) in the collection of the South African Museum with a skull length of approximately 86 mm., the 1st, 3rd and 5th teeth appear to have been the younger.

The additional material shows that the series available to Parrington covered only part of the growth series and that the individual postcanines were replaced several times. The additional growth stages are shown in figure 11 A, stages I and IV. Stage I represents specimens A and B in which the 2nd, 4th and 6th are the youngest. The older teeth in stage I have been numbered 1 and the younger teeth 2. By the time stage IV is reached the teeth numbered 1 have been replaced twice and, therefore, the teeth in the corresponding positions have been numbered 3. The teeth numbered 2 in stage I are replaced once and the teeth in the corresponding position in stage IV are, therefore, numbered 3. It is, however, apparent from an analysis of the postcanine teeth of the specimens available that in *Thrinaxodon* the replacement pattern is more complex than the simple alternation shown in figure 11 A. Further detailed consideration of the specimens is therefore necessary.

Posterior migration of the postcanine row

The number of postcanines in the jaws studied varies slightly. In many cases remnants of postcanines are present in front of the functional postcanines and in some cases unerupted or partially erupted teeth are present behind the functional row. In some cases these teeth do not appear to have had predecessors. This information is summarized in table II. The number of functional teeth appears to be fairly constant. All the maxillae, with the exception of specimen A, have six functional teeth and all the mandibles with the exception of specimens D and G have seven functional postcanines.

TABLE II

	UPPER POSTCANINES				LOWER POSTCANINES			
	Anterior tooth remnants	*No. functional p.c.*	*Unerupted posterior p.c.*	*Total*	*Anterior tooth remnants*	*No. functional p.c.*	*Unerupted posterior p.c.*	*Total*
A		7		7				
B		6		6				
C		6		6	(1)	7	(1)	9
D		6		6	(1)	8		9
E		6	(1)?	7	(1)	7	(1)	9
F		6	(1)	7	(1)	7	(1)	9
G		6	(1)	7		8		8
H		6	(1)	7		7		7

The constant number of functional postcanines in most specimens, the frequent occurrence of a tooth remnant anterior to the functional row and the presence behind the postcanine row of an unerupted postcanine which does not appear to have had a predecessor, suggest that during growth the anterior postcanines were lost and that new postcanines were added posteriorly. In mandibles of specimens C, E, F and G (figs. 2, 5, 6 and 9) it would be expected in terms of alternate tooth replacement that the 1st functional tooth would be a younger tooth erupted shortly before death or at least that it would have a well-developed replacing tooth in a pit at its base. This is not the case. In all four specimens the first functional tooth is firmly held by attachment bone and there is no indication of a replacing tooth at its base. The fact that the first functional tooth was not about to have been replaced in these four specimens suggests that in a more advanced growth stage the first functional tooth became the tooth remnant anterior to the postcanine row which is preserved in some specimens. This fact supports the conclusion that postcanines were lost anteriorly and added posteriorly during growth. In other words, the functional row of postcanines migrated backwards during growth. This appears to be so arranged that the number of functional postcanines remained roughly constant during growth. An explanation of this nature could account for the varying postcanine count attributed to *Thrinaxodon* in the literature. For example, if in the lower jaw the new tooth behind had erupted sufficiently to be considered part of the functional row the number would be given as eight, if not as seven. In figure 11 B, a series of growth stages are shown in which teeth are progressively lost in front and added behind. This has been superimposed upon the simple alternate replacement shown in figure 11 A. Although this model appears to be theoretically sound it only agrees with the state of eruption of the postcanines in some of the specimens, to wit those in which the 2nd, 4th and 6th postcanines are replacing. If teeth were added and lost in the manner suggested in figure 11 B, the state of the postcanine row at each growth stage would appear to be identical, i.e. it would always appear that the 2nd, 4th and 6th teeth were replacing because teeth are added and lost at the same rate. This is clearly not the case as specimens are also available in which the 1st, 3rd and 5th teeth are replacing.

Posterior migration of the postcanine row appears to be a characteristic of many of the advanced cynodonts, e.g. *Scalenodon* (Crompton, 1955); South American gomphodont cynodonts (Patterson and Olson, 1961) and *Diademodon* (Fourie, 1963).

There is ample evidence that the canines replaced several times. As the replacing canines were larger than their predecessors the new teeth invaded the region occupied by the anterior postcanine. It appears that in order to compensate for the loss of anterior postcanines further teeth were added at the back of the tooth row.

Replacement cycle

In figure 12 an attempt has been made to fit the postcanine rows of the specimens studied into an orderly sequence. This series indicates how posterior migration of the postcanine row was achieved in such a way that in some specimens the odd-numbered teeth are replacing and in others the even-numbered teeth are replacing. The upper postcanines are shown in figure 12 A and the lower postcanines in figure 12 B. In this figure teeth drawn in dotted lines above the alveolar border in the upper jaw and below it in the lower jaw had not yet erupted.

The first growth stage (I) in the series in figure 12 A is a diagrammatic representation of the upper postcanine row in specimen H (fig. 10). The 2nd, 4th and 6th teeth are in the process of erupting, but the 6th is further erupted than the 2nd or 4th (replacement wave). Replacement teeth are present above the 3rd and 5th postcanines, but not above the 1st. An unerupted tooth is present behind the 6th in position 7. There was no functional predecessor for this tooth. It is larger than the replacing tooth at position 5.

In specimen A (stage I A on the right of fig. 12 A) seven teeth are present, of which the 2nd, 4th and 6th are the youngest. It is possible that the state of the postcanine row in specimen A is similar to that of H except that the unerupted postcanine in position 7 has erupted and is functional.

In a later growth stage (fig. 12 A, II) the 1st functional postcanine which had no replacement tooth in stage I has been shed. The partially erupted 2nd, 4th and 6th postcanines of stage I are now fully erupted. Because one postcanine has been lost the 2nd, 4th and 6th of stage I become the 1st, 3rd and 5th of stage II. Consequently the replacing teeth that were developing in stage I above the 3rd and 5th replace the previous teeth and erupt in stage II as the 2nd and 4th. The unerupted additional tooth (position 7) of stage I erupts as the 6th in stage II. Consequently although in both stages I and II the 2nd, 4th and 6th teeth are the youngest, the teeth referred to are not the same in both stages.

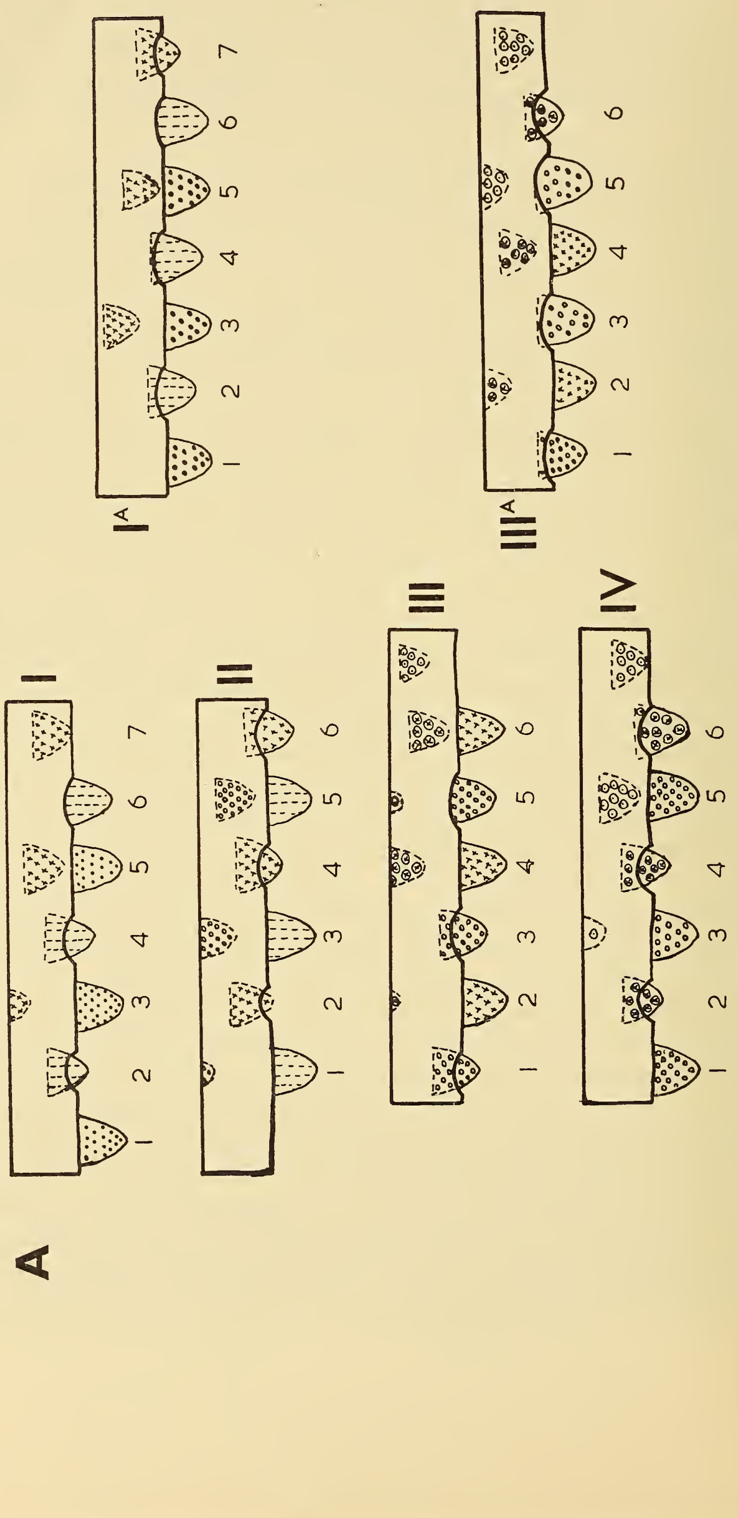
Replacing teeth are developing above the 1st, 3rd and 5th teeth in stage II. Stage II appears to correspond with specimen B. In this specimen there is no indication of an unerupted tooth behind the functional postcanine row. As the functional 1st, 3rd and 5th in specimen B are considerably larger than the corresponding teeth in specimen A, several growth stages probably separated these two specimens. This point will be considered again later.

In stage III the replacing teeth developing above the 1st, 3rd and 5th postcanines in stage II have erupted. In stage II replacing teeth are erupting in the 2nd, 4th and 6th alveoli. In stage III these are fully erupted. An additional tooth is developing behind the functional row and the development of a replacing tooth for the 5th has commenced. The state of eruption and replacement of the postcanines in this stage corresponds exactly to that present in specimens E and F (figs. 5 and 6). Specimens C, D and G appear to be slightly in advance of stage III because the replacing tooth for the 6th postcanine has erupted and replaced the old functional tooth in this position. This is illustrated in stage III A on the right of figure 12 A. Stage III is followed by a stage IV. Apart from the fact that the first functional tooth is now one position further back, this stage is identical to I, thereby completing the cycle.

The replacement cycle (fig. 12 B) in the lower jaw is basically the same as that concluded to have been present in the upper jaw. The only real difference is that the number of functional teeth is seven instead of six.

In growth stage I (fig. 12 B) the 1st, 3rd, 5th and 7th teeth are in the process of erupting. Replacing teeth are developing below the 2nd, 4th and 6th postcanines. This stage corresponds with the postcanine row of specimen H. In the right mandible of this specimen the old functional first tooth had not been shed, but it was shed on the left. This tooth has been indicated by a dotted outline in stage I. In specimen H there is no indication of an unerupted postcanine behind the last functional tooth. Specimen D (fig. 3 B) corresponds with stage I in regard to the state of eruption of the first seven postcanines, but a small 8th tooth is present behind the postcanine row. The state of eruption of the postcanines in specimen D is shown diagrammatically in stage I A (on the right-hand side of fig. 12 B). This specimen is discussed in more detail below.

In stage II the replacing teeth which were developing below the 2nd, 4th and 6th in stage I are erupting and replacing teeth are developing for the 3rd, 5th and 7th postcanines, but not for the first postcanine. An unerupted tooth is developing behind the 7th postcanine. The 1st, 3rd, 5th and 7th teeth that


A
I
1 2 3 4 5 6 7
II
1 2 3 4 5 6
III
1 2 3 4 5 6
IV
1 2 3 4 5 6
IA
1 2 3 4 5 6 7
IIIA
1 2 3 4 5 6

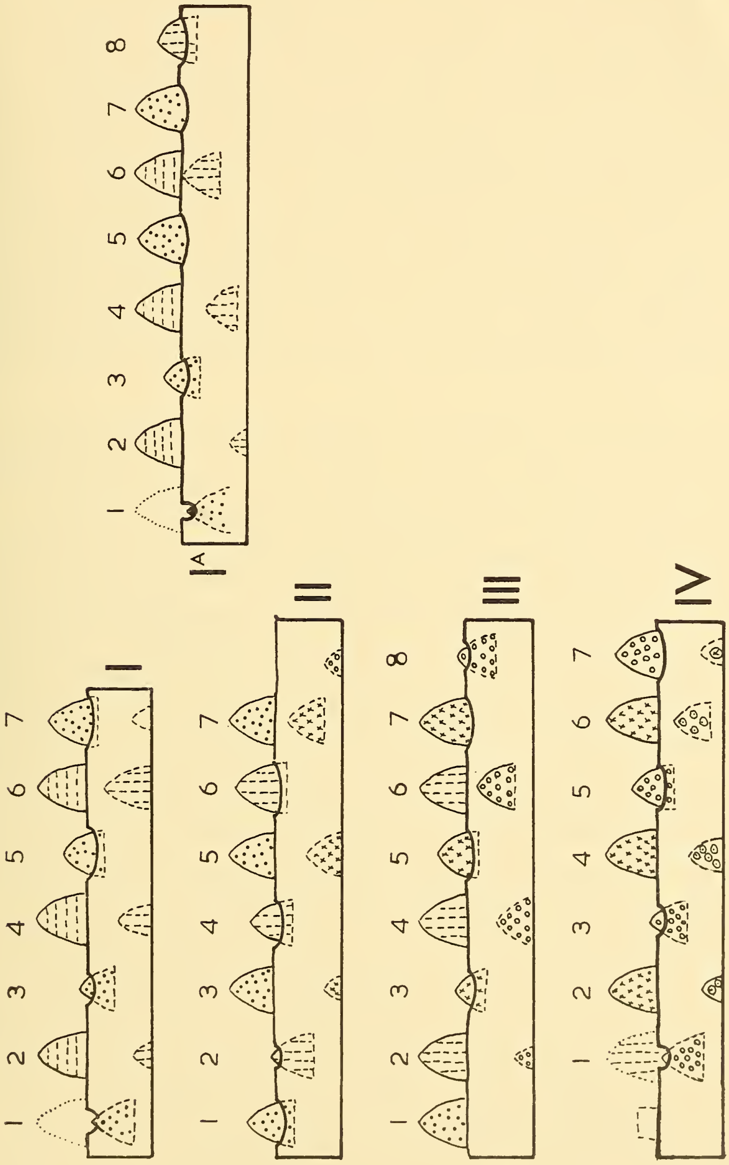


FIG. 12. *Thrinaxodon* sp. Replacement cycle of all the postcanines. A, upper and B, lower.

were partially erupted in stage I have in stage II erupted further. The 7th is fully erupted, but the 1st is only partially erupted. This stage is not represented in the material studied. In stage III the partially erupted 1st postcanine of stage II is fully erupted and retained. The other odd-numbered, functional teeth (3rd, 5th, 7th) of stage II have, however, been lost in stage III and their replacing teeth which were developing in stage II are now erupting. The retention of the 1st postcanine in stage III is presumably correlated with this tooth having no successor and being younger than the other functional odd-numbered teeth in stage II. Replacing teeth are developing below the 2nd, 4th and 6th postcanines and a partially erupted tooth is present behind the functional row. This stage corresponds with the postcanine row in specimens C, E and F (figs. 2, 5 and 6). In these specimens the remnant of a tooth is visible anterior to the functional postcanine row. This is discussed below. Specimen G (fig. 9 A) is similar to stage III in the state of eruption of the first five postcanines, but the partially erupted 8th postcanine shown in stage III is fully erupted.

The next stage, IV, is identical to I, except that the first functional tooth is one position further back. The 1st postcanine of stage III which has no replacing tooth, is retained as a tooth remnant. This remnant would presumably have been retained in the next three stages of the replacement cycle.

Edmund (1960, 1962) has made a thorough study of tooth replacement in reptiles. He has shown that the spacing between hypothetical impulses which initiate the development of teeth and which travel along the free margin of the dental lamina can account for the fact that in some reptiles the replacement pattern is strictly alternate, whereas in others waves of replacement pass from back to front or front to back along alternately numbered tooth series. Back to front waves are present in all the specimens of *Thrinaxodon* studied. Edmund has shown that the basic units in the dentition of all reptiles are *Zahnreihen*. He has suggested that Bolk's term 'Odontostichi' be dropped. *Zahnreihen* consist of a series of teeth that are either the 1st, or the 2nd, or the 3rd, etc., teeth developed from successive tooth positions, e.g. all the first teeth to develop at each successive tooth position form the 1st *Zahnreihe*, all the second teeth, the 2nd *Zahnreihe*, and so on. Development of teeth at each tooth position is iniated by an impulse travelling backwards along the free margin of the dental lamina. The spacing between successive impulses determines the spacing between successive *Zahnreihen*. Edmund has shown that the functional dentition in reptiles is the product of several *Zahnreihen*. In order to obtain a complete dentition many members of each *Zahnreihen* must be discarded or resorbed, for example, as Edmund has shown in a dentition consisting of 21 positions, '. . . 15 members of the first *Zahnreihe* are discarded before the first anlage of position twenty-one is laid down, and many members of the first seven *Zahnreihen* must be discarded before the first mature tooth is produced at position twenty'.

The type of replacement which took place in *Thrinaxodon* is basically the same as that which takes place in living reptiles. Therefore, the postcanine row of *Thrinaxodon* also probably consisted of the products of several *Zahnreihen*. It should, therefore, be possible to account for cycle of replacement concluded to have taken place in the postcanine row of *Thrinaxodon* in terms of Edmund's theory of the development of the functional dentitions of reptiles.

In figure 13 an attempt has been made to reconstruct the ontogenetic stages which led up to the development of the functional lower postcanine row. These are illustrated in figure 13 A to G. Subsequent changes in the postcanine row which were concluded in the section above to have taken place are shown in figure 13 H to L. The embryonic stages were deduced by working back from figure 13 H in terms of Edmund's theory.

In a hypothetical early stage, figure 13 A, the first impulse to travel along the free margin of the dental lamina is shown at position no. 1. It has initiated the development of the first tooth at this position. The first impulse is indicated as an arrow followed by the number 1. In a later stage (fig. 13 B) the impulse has moved to tooth position 2 and initiated the development of a tooth at this position. The tooth at position 1 is larger. In figure 13 C the first impulse has passed position 3 where it initiated the development of a tooth. A second impulse, 2·5 tooth positions behind* the first impulse, has initiated a second tooth at position 1. In a later stage, figure 13 E, this second impulse is 2·5 tooth positions in front of tooth position 1 and a third impulse commences in position 1. In figure 13 G the third impulse has initiated the development of the 3rd tooth at tooth position 3. Three teeth have, therefore, been formed at teeth positions 1, 2 and 3. The second impulse is 2·5 tooth positions in advance of the third impulse and two teeth have been formed in positions 4 and 5. The first impulse has initiated a tooth at tooth position 8 and one tooth has, therefore, been formed at tooth positions 6, 7 and 8.

In figure 13 H, the 4th impulse has initiated the development of a tooth at position 2, 2·5 tooth positions behind the 3rd impulse. The 4th impulse did not initiate the development of a tooth at position 1. The 1st impulse has faded out and no further teeth are initiated at this stage behind tooth position 8. In figure 13 H the alveolar border is indicated. The parts of the functional teeth above the alveolar border have been drawn in black. Unerupted teeth have been drawn in dotted outline. The teeth drawn in outline only above the functional teeth are the teeth that were resorbed or shed during development. Figure 13 H corresponds to stage III of the replacement cycle shown in figure 12 B, i.e. similar to the arrangement of the postcanines in specimens C, E, and F. In figure 13 H the functional postcanine row is built up of the teeth belonging to the first three *Zahnreihen* (Z1, Z2 and Z3). Five teeth have been lost from the first *Zahnreihe* and three from the 2nd *Zahnreihe*. Development of the 4th *Zahnreihe* (Z4) has commenced. The 1st, 2nd and 3rd functional teeth are the third teeth to have developed in these positions and are part of the 3rd *Zahnreihe*. The 4th, and 5th are the second teeth to have developed in this

*The word 'behind' is used with reference to the direction of migration of the hypothetical impulse. Since the latter is moving from back to front, 'behind' means 'anterior to'.

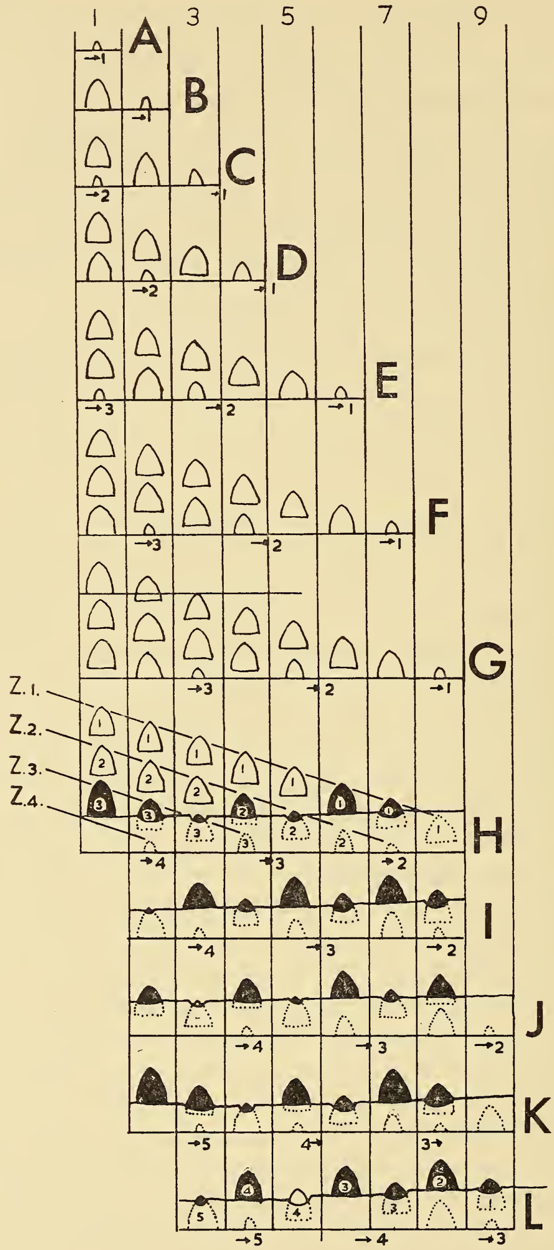


Fig. 13. *Thrinaxodon* sp.

Diagram to illustrate hypothetical development stages (A–G) leading up to a functional lower postcanine row (H) and the subsequent replacement cycle (I–L). Based upon Edmund's theory.

position and form part of the second *Zahnreihe*. The 6th and 7th teeth are the first to have developed in these positions and form part of the first *Zahnreihe*.

In a later growth, figure 13 I, the 1st functional tooth of figure 13 H is lost and no new tooth is present in this position. Therefore, the tooth in position 2 in figure 13 I is the first functional tooth. Figure 13 I is the same as stage IV or I in figure 12 B. In this stage the condition of the postcanine row is as in specimen H. In figure 13 I, the 4th impulse has initiated a tooth in position 3 (i.e. beneath the 2nd functional tooth). The 3rd impulse has initiated a tooth in position 5 and the 2nd impulse has initiated a tooth in position 8. Figure 13 J is equivalent to stage II in figure 12 B. Figure 13 K corresponds to stage III in figure 12 B and the 2nd, 3rd and 4th impulses have moved one tooth position backwards. Figure 13 K is a repetition of figure 13 H. In the former the 2nd impulse has faded away and the 5th impulse has initiated a tooth at tooth position 3 (functional 2). Figure 13 L is a repetition of figure 13 I. In figure 13 L the partially erupted tooth in position 3 is the first functional tooth. Thus Edmund's theory of successive impulses which initiate teeth and travel along the free margin of the dental lamina can account for the replacement cycle for the postcanine series concluded to have taken place in the lower jaw of *Thrinaxodon*.

We must now return to consider specimen D, which is peculiar in possessing eight functional lower postcanines. Furthermore the extra tooth, instead of being large, is small and simple. On the basis of a scheme of the type shown in figure 13, it is possible to account for these peculiarities. It can be assumed that in the development of specimen D, when a stage similar to figure 13 H was reached, the first impulse did not fade away but initiated a tooth at position 9. A tooth initiated in this stage would become functional in a later stage similar to figure 13 I. With the exception of the additional tooth, the state of eruption of the individual postcanines in specimen D is similar to that shown in figure 13 I. It is possible to account for the simple crown pattern of this tooth if it is assumed that its crown was formed behind the point where the morphogenetic gradient for 'molarization' was at its maximum (see p. 513).

If Edmund's scheme is followed it is also possible to account for the replacement cycle concluded to have taken place in the upper postcanines. These are shown in figure 14. The first stage shown (fig. 14 A) corresponds exactly with figure 13 G. It is unnecessary to repeat the stages leading up to figure 14 A as these correspond to those shown in figure 13. For convenience the teeth in figure 14 are orientated pointing downwards, to indicate that they are upper teeth. The postcanine row in figure 14 A consists of six functional teeth and an unerupted tooth behind. This row consists of the products of three *Zahnreihen* (Z^1 to Z^3). The 2nd impulse has initiated a tooth at position 5 and the 3rd impulse a tooth at position 3. The stage represented in figure 14 A is the same as stage I in figure 12 A. In a later stage, figure 14 B, which corresponds to stage II in figure 12 A the 1st functional tooth has been shed and no new tooth has been initiated in this position. The 1st tooth initiated by the 4th impulse is present at tooth position 2. In figure 14 C, which corresponds with stage III in figure 12 A, the 2nd impulse has initiated a new tooth in position 8, and the 3rd a tooth in position 5 and the 4th a tooth in position 3. Figure 14 D is identical to figure 14 A, except that the tooth row has moved one tooth position backwards. After the stage shown in figure 14 C the 2nd impulse

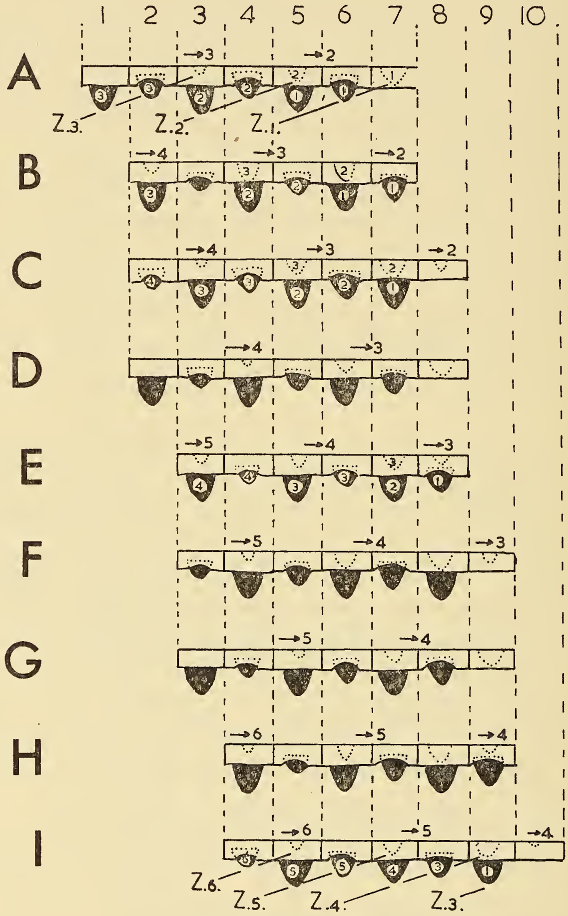


Fig. 14. *Thrinaxodon* sp.
Diagram to illustrate the application of Edmund's theory of tooth replacement to the replacement cycle for the upper postcanines.

appears to fade away. In figure 14 E to I the replacement cycle is continued. In figure 14 E the 5th impulse has initiated a tooth in position 3. In figure 14 H the 6th impulse has initiated a tooth in position 4.

It is thus possible to account for the state of eruption and replacement of individual postcanines and the posterior migration of the postcanine row in several specimens of *Thrinaxodon* if it is assumed that:

(1) regular impulses, 2·5 tooth spaces apart, travel caudad along the free margin of the dental lamina;

(2) each new impulse commences one tooth position behind the tooth position where the previous impulse commenced.

The sequence of a replacement in successive growth stages shown in figure 12 was based upon the state of eruption of the individual postcanines in a number of actual specimens. It is important that this sequence agrees with the sequence based upon Edmund's theory and shown in figures 13 and 14.

Once the replacement cycle is determined it is possible to estimate the minimum number of times each postcanine was replaced. The youngest specimen known (specimen A) appears to correspond with the stage shown in figure 14 A. The 1st and 2nd teeth of this stage are apparently the third teeth to have developed in these positions, the 3rd and 4th are the second, the 5th and 6th, the first at their respective positions. The state of eruption of the postcanines of specimen B corresponds with the stages shown in figure 14 B, E and H. As there is a considerable difference in the size of the individual postcanines of specimens A and B (see fig. 1) it is not possible for specimen B to have been the immediate successor of a specimen similar in size to that of specimen A. Therefore, several growth stages probably separate specimens A and B. If specimen A is equated with figure 14 A it is reasonable to equate specimen B with figure 14 E. Figure 14 F corresponds with specimens C, D, E, F and G and Parrington's specimens E, F, G (see table I). Specimen H and Parrington's I corresponds with figure 14 G. A specimen corresponding with figure 14 H is not known. Specimen I corresponds with figure 14 I. In figure 14 I the 1st functional tooth corresponds with tooth position 4. The postcanine row in figure 14 I is made up of the members of the 3rd, 4th, 5th and 6th *Zahnreihen* (Z^3–Z^6). The 1st functional postcanine (i.e. the tooth at tooth position 4) is the 6th tooth to develop in this position, the 2nd and 3rd functional are the 5th to develop in these positions, the 4th functional is the 4th tooth to develop in this position, the 5th functional tooth is the 3rd tooth to develop in this position and the 6th functional the 1st to develop in this position.

This means that the 1st functional tooth of an old specimen has been replaced at least five times, the 2nd and 3rd, four times, the 4th, three times, the 5th, twice, and the 6th not replaced. The fall off in the number of replacements in a posterior direction is correlated with the posterior migration of the postcanine row.

Differentiation of the postcanine row

A characteristic of *Thrinaxodon* is the increase in the complexity of the crown pattern in a posterior direction. The anterior postcanines are 'caniniform' in appearance and the crown is dominated by the main cusp whereas the posterior teeth have a complex 'molariform' pattern not unlike that of some early mammals. It has already been shown (Crompton, 1963) that *Thrinaxodon* was one of the earliest of the mammal-like reptiles which was capable of a sustained bite across the postcanines. The power of this bite was greatest across the posterior region of the postcanine row and it is possible to correlate the complex postcanines in this region with this fact. The simple pattern of anterior postcanine teeth was possibly correlated with their position close to the canine. If the anterior teeth had complex crowns they would have interfered with the stabbing action of the canines to a greater extent than simple 'caniniform' postcanines.

In most of the specimens studied the postcanines do not all form a graded series in which each postcanine is slightly more molariform than the tooth immediately in front of it. Usually it is possible on the structure of the crowns divide the postcanine row into two series, one consisting of partially erupted

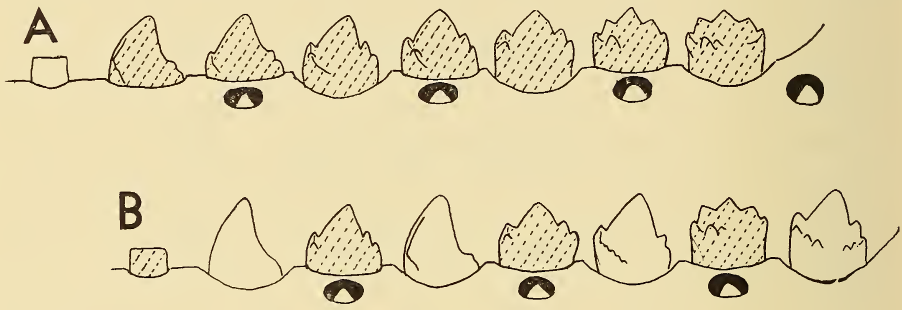


FIG. 15. *Thrinaxodon* sp.
Posterior migration and differentiation of the lower postcanines.

postcanines and one consisting of the fully erupted postcanines. The series are alternately numbered, i.e. the teeth numbered 3, 5 and 7 form one series and the teeth numbered 2, 4, 6 form the other series. In each of these series there is a progressive complication of the crown structure in a posterior direction. One of the major differences between the crown structure of the two series is that the partially erupted teeth have simpler crown patterns (or were more caniniform) than the fully erupted teeth immediately anterior or posterior to them. During growth postcanines are lost from the front of the row and others are added behind. Consequently if differentiation of the postcanine row into simple postcanines anteriorly, and complex postcanines posteriorly, is to be maintained during growth each tooth must be replaced by a tooth with a simpler crown pattern. This is illustrated in figure 15. The stage of the replacement cycle shown in figure 15 A corresponds to figure 13 H and that shown in figure 15 B corresponds to that shown in figure 13 I. The tooth developing below the second functional in figure 15 A would become the 1st functional tooth in the later stage, figure 15 B. It must therefore be more caniniform than the tooth it replaces. This explanation could account for minor differences between adjacent teeth, but in fact the differences are far greater than could be accounted for in this way. It has been noted above that it is possible to divide the row up into two series. Teeth belonging to one series have different crown patterns from teeth belonging to the other series. The differences between the two series in specimen D are described in detail on p. 486.

The complication of the teeth in a posterior direction suggests that they develop under the influence of a morphogenetic gradient, in the manner which has been suggested by Butler (1939) for mammalian dentitions. Butler postulates

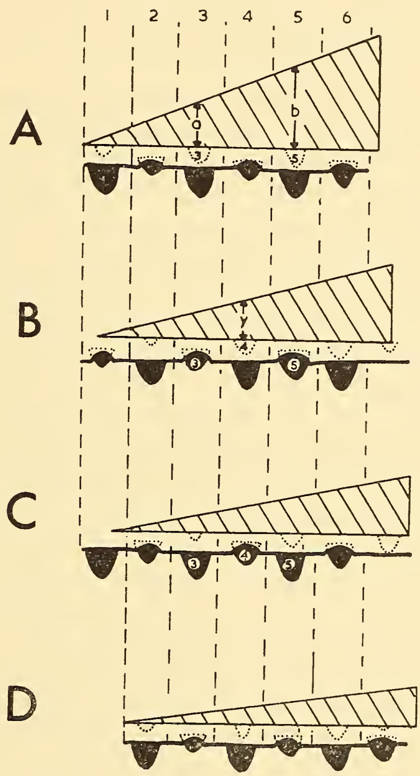


FIG. 16. *Thrinaxodon* sp.
Diagram to illustrate posterior migration and changes in the morphogenetic gradient responsible for the structure of the lower postcanines.

a short steeply graded field of 'caninization' determining the form of the canine tooth, succeeded by and slightly overlapping a longer, more gently graded molarization field, affecting the entire postcanine row. The teeth immediately behind the canine will therefore show little molarization since they develop under the influence of the low anterior end of the molarization gradient and are also slightly affected by the caninization field. Further back the canine field vanishes and the molarization field becomes increasingly strong, so that the teeth become progressively more molarized from front to back of the postcanine row. In figure 16 the morphogenetic gradient of the molarization field in a series of growth stages has been shown diagrammatically. For simplicity sake the caninization field is not shown. It can be imagined as lying directly in front of the 1st postcanine and fading out rapidly, so that its influence does not extend beyond the 1st postcanine. During growth the gradient migrates in a posterior direction. In figure 16 A the gradient commenced at tooth position 1. In figure 16 D the gradient had shifted to tooth position 2. In the intervening stages a gradual shift of the gradient in a posterior direction presumably took place.

In specimens C, D, E and F the most molariform teeth in the lower jaw have well-developed cingular cusps and the main cusps are about the same size as the accessory cusps. In the larger specimen G the most molariform tooth is less molariform than those in specimens C, D, E and F. In this tooth the cingular cusps are well developed, but the main cusp is relatively larger. In the larger specimen H, the most molariform tooth is less molariform than that of specimen G. The main cusp is large and the cingular cusps are poorly developed. This suggests that the morphogenetic gradient is very steep in early stages, but levels off in later growth stages. In the four growth stages shown in figure 16, this feature is shown diagrammatically. The replacing teeth for 1st, 3rd and 5th teeth in stage A develop when the gradient is steep and commences at tooth position 1, whereas the replacing teeth for the 2nd, 4th and 6th teeth develop at a later stage, B, when the gradient is further posterior and is less steep. The replacing teeth developing in stages A and B form the functional post-canines in stage C. The structure of the crowns of 1st, 3rd and 5th in stage C increases in complexity in a posterior direction, but despite this their crown patterns are distinct from those of the 2nd, 4th and 6th. It may be possible to correlate this with the fact that the two series developed under different gradients occupying different positions. Take, for example, the 3rd, 4th and 5th functional postcanines in stage C. The 4th tooth is formed in stage B. The strength of the gradient at this point in stage B has been indicated and labelled Y. The 3rd and 5th functional teeth of stage C are formed in stage A. The strength of the gradient affecting these teeth is indicated and labelled *a* and *b*. As *a* and *b* are both larger than *y* the 3rd and 5th teeth will be more molariform than the fourth.

This conclusion is highly speculative and well-prepared additional material is required to confirm these results. If it is correct it would explain why a recently erupted tooth has a simpler and different crown pattern than the postcanines anterior and posterior to it. It is of some interest that the changes in the ontogeny of *Thrinaxodon* are of essentially the same type as Butler (1939) suggests have been operative during mammalian phylogeny.

In the descriptive section the specimens were divided into three groups. This division was based on the structure of the postcanine teeth in the mandible. The different crown patterns are correlated with skull length, and it is therefore possible that these differences are related to changes which the morphogenetic gradient undergoes during growth. Consequently these differences probably have no taxonomic importance. Until this is confirmed or denied no attempt should be made to place the different groups in different species.

Notes on the postcanine row of Gomphodont cynodonts

Diademodon is characterized by a differentiated postcanine row (Brink, 1955*a*, 1957; Crompton, 1955). Three distinct regions can be recognized in both upper and lower jaws—an anterior, central and posterior. The three to four postcanines of the anterior region have simple conical crowns with a slight development of a cingulum on the lingual edge. These teeth are small in comparison with the remaining postcanines. The central region consists of about seven postcanines with transversely ovate gomphodont crowns. In this region wear of the crown surfaces decreases progressively in a posterior direction. The size of the crowns increases progressively in a posterior direction. The posterior region consists of about four teeth. In this region the crowns become progressively more longitudinally ovate in a posterior direction. Fourie (1963) has referred to the crown patterns of these four teeth as 'intermediate gomphodont', 'intermediate sectorial', 'large sectorial' and 'small sectorial'.

Diademodon specimens covering a wide size range are known. In all specimens the postcanine row is differentiated in the same way and in all the specimens the postcanines of the central region are characterized by a progressive decrease, in a posterior direction, of the wear of the crown surfaces and a progressive increase, also in a posterior direction, of size. Brink (1957) has noted '. . . that replacement would tend to cause an irregular series of differently sized teeth'. An irregular series of postcanines in the central region has never, to the author's knowledge, been observed in *Diademodon*.

The teeth of the central region are considerably larger in older specimens of *Diademodon* than in younger specimens. Tooth replacement must therefore have occurred in this region. Replacement must have taken place in such a way that the postcanines of both the central and posterior regions always formed a graded series. How was this achieved? In order to answer this question it is necessary to review the evidence of replacement of the postcanines in *Diademodon*.

Fourie (1963) has found evidence for the loss of anterior postcanines during growth. He has also found unerupted postcanines which had no predecessor behind the functional postcanines. He has concluded that during life the postcanine row migrated posteriorly. The number of functional teeth remained constant as teeth were lost and added at roughly the same rate. Broom (1913) has reported replacement of some of the anterior conical postcanines by new conical postcanines. Fourie will also describe several specimens showing replacement in this region.

In a specimen of *Diademodon* housed in the Geologish-Paläontologisches Institut und Museum in East Berlin the right maxilla contains two conical anterior postcanines. These are followed by a small, greatly worn transversely ovate postcanine. This tooth is the first of the central region consisting of postcanines with transversely ovate crowns. In the left maxilla three and not two anterior postcanines with sharply pointed conical crowns are present. The posterior of the three appears to have erupted shortly before death and shows no sign of wear. There is no doubt that numerically this tooth corresponds with the greatly worn transversely ovate postcanine in the right maxilla. This suggests that replacement in the left maxilla was in advance of that in the right and also that a simple conical postcanine replaced a transversely ovate postcanine. The author (1955) has reported the replacement of the 6th postcanine (second postcanine of the central region) in *Diademodon*. The replacing tooth appears to be more conical than transversely ovate.

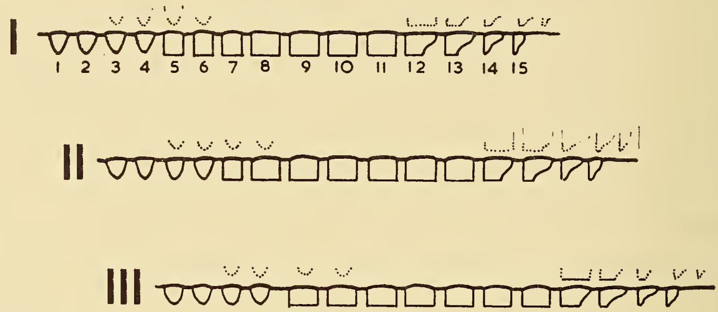


FIG. 17. *Diademodon* sp.
Diagram to illustrate replacement and posterior migration of the postcanine row.

The author (1955) has also claimed that in two specimens of *Diademodon* one of the upper longitudinally ovate sectorial postcanines in the posterior region was replaced by a tooth with a gomphodont crown pattern. This claim was based upon the fact that a longitudinally ovate foramen which follows immediately after an alveolus for a gomphodont tooth is present in these specimens below the unerupted gomphodont postcanine. This foramen was interpreted as an alveolus for a sectorial postcanine. Brink (1957) has challenged this view and has offered an alternative interpretation for the longitudinally ovate foramina behind the functional postcanine row. He has claimed that '. . . these openings could equally well be interpreted as ordinary gubernacular canals'. I find this interpretation difficult to accept for two reasons: (1) in most specimens of *Diademodon* the postcanine row is terminated by sectorial postcanines; (2) replacement of sectorial teeth by gomphodont teeth at the back of the postcanine row has also been reported in *Cricodon* (Crompton, 1955) and in *Trirachodon* (Parrington, 1960). Fourie (1963) has confirmed the replacement of sectorial teeth by gomphodont teeth at the back of the row in *Diademodon*. He has shown that the 'intermediate gomphodont postcanines' are replaced by 'gomphodont'; the 'intermediate sectorial' by 'intermediate gomphodont' and, 'large sectorial' by 'intermediate sectorial', a 'small sectorial' by 'large sectorial'.

In figure 17 the information listed above has been applied to a growth series of *Diademodon*. In the first growth stage I the postcanine row consists of fifteen teeth. The 1st to the 4th are conical, the 5th to the 11th are gomphodont. In a posterior direction the latter increase progressively in size and wear decreases progressively. The 12th is intermediate gomphodont, the 13th intermediate sectorial, the 14th large sectorial and the 15th small sectorial. There is evidence that the 1st and 2nd postcanines were lost, that the 3rd–6th and 12th–15th postcanines were replaced and that teeth were added posteriorly. If teeth are lost anteriorly and added posteriorly then it follows that if the differentiation of the postcanine row is to be maintained that:

(1) the 3rd and 4th postcanines must have been replaced by conical teeth;

(2) the 5th and 6th postcanines must have been replaced by conical teeth;

(3) the 12th postcanine must have been replaced by a gomphodont tooth; the 13th by an intermediate gomphodont; the 14th by intermediate sectorial and the 15th by a large sectorial;

(4) the new tooth at the back of the row must be a small sectorial type.

All this is in agreement with the available evidence. If replacement of this nature is repeated differentiation of the postcanine row will be maintained throughout the period of growth. The crowns of the central region will always form a graded series because as greatly worn anterior teeth of the series are replaced by conical teeth new unworn gomphodont teeth are added behind.

The description above accounts for the maintenance of a fully differentiated postcanine row, and it is interesting to speculate on the growth stages that led up to the formation of a fully differentiated postcanine row. The youngest *Diademodon* specimen that has been described (Fourie, 1963) already has a fully differentiated row. In this specimen, however, there is no evidence that teeth had been lost anteriorly. The progressive increase of the wear of the crowns of the central region suggests that during growth these teeth were added one after the other after the animal had started to use its teeth. This implies that *Diademodon* commenced active life with only a few teeth. This also suggests that the posterior region of the row was only added after a full complement of gomphodont teeth had erupted. As mentioned above the youngest available specimen does not appear to have lost anterior teeth. This may suggest that replacement only commenced after a complete postcanine dentition had erupted.

The above discussion of the growth of the postcanine row is highly speculative, but the available evidence on the growth of the postcanine row of Middle Triassic cynodonts tends to confirm at least some of the conclusions reached above. A good growth series of the jaws of *Scalenodon* has been described (Crompton, 1955).

The youngest available specimen of *Scalenodon* has five postcanines. These are all transversely ovate and wear decreased in a posterior direction. Conical anterior postcanines are not present. During growth postcanines were added progressively behind to increase the length of the postcanine row. The largest specimen has eleven postcanines. Sectorial teeth were only added at an advanced growth stage. These were replaced by transversely ovate teeth. Teeth were lost in front during growth. This process appears to have commenced at an early stage, but appears to have been slower than addition behind.

Olson and Patterson (1961) have stated that in undescribed South American cynodonts teeth were also lost anteriorly and added behind. Kühne (1956) has made a similar observation in the tritylodontid *Oligokyphus*.

In no gomphodont cynodonts is there any indication of alternate replacement in the postcanine row. It appears rather that postcanines are added progressively from front to back and that some of these teeth are progressively replaced. In *Diademodon* some of the anterior and posterior postcanines are replaced, in *Scalenodon* only posterior postcanines are apparently replaced and in *Oligokyphus* none of the cheek teeth were replaced.

In most placental mammals teeth are laid down progressively from front to back. Edmund (1960) has pointed out that as the deciduous dentition and the molars are the first teeth to be formed in the positions they occupy, they constitute a single *Zahnreihe*. The permanent incisors, canines and premolars constitute a second *Zahnreihe*. In *Thrinaxodon* and other early cynodonts the products of several *Zahnreihen* function simultaneously and alternate replacement is present. The absence of alternate replacement in gomphodont cynodonts and the progressive addition of teeth suggest that gomphodont cynodonts paralleled to some extent later development in mammals. Large sections of the functional postcanine row of *Diademodon* appear to form part of a single *Zahnreihe* since teeth were added progressively without anterior replacement. Teeth numbered 1 to 15 in figure 17 (I) may constitute a single *Zahnreihe*. The teeth that replaced them may constitute a second *Zahreihe* of which the central members had been suppressed.

Summary

1. Tooth replacement is described in eight specimens of the cynodont *Thrinaxodon liorhinus* Seeley. It is shown that replacing teeth developed in pits lingually to the functional teeth. During growth the replacing teeth migrated labially to lie below the crowns of the functional teeth. It is concluded that the replacement cycle of individual teeth is identical to that reported for *Ericiolacerta* (Crompton, 1962).

The replacement cycles of the entire postcanine row (both upper and lower) are deduced from the state of eruption of the individual postcanines of the specimens studied.

2. Parrington's (1936) observation that the teeth replaced alternately is confirmed. It is shown that a wave of replacement passed from back to front along both the odd and even numbered postcanines.

3. The loss of anterior postcanines and the addition of further teeth at the back of the row resulted in a posterior migration of the functional postcanine row. This was probably correlated with the increase in size of each successive replacing canine.

The stages at which teeth were lost anteriorly and added posteriorly is illustrated.

It is shown that Parrington's (1936) series of *Thrinaxodon* only covered part of the growth period. Older and younger specimens are described.

4. It is shown that it is possible to interpret the replacement cycle in *Thrinaxodon* in terms of Edmund's (1960) interpretation of reptilian tooth replacement. It is shown that in *Thrinaxodon* erupting postcanines usually had simpler (less molariform) teeth than the fully erupted postcanines immediately anterior or posterior to them. It is suggested that the posterior migration of the postcanine row can only partially explain this phenomenon.

It is suggested that the postcanines of *Thrinaxodon* developed under the influence of a morphogenetic gradient (Butler, 1939). Teeth developed under the influence of the anterior portion of the gradient were 'caniniform' and those developed under the posterior portion of the gradient 'molariform'. It is suggested that in the early stages the gradient was steep, but that in older specimens the gradient levelled off and moved progressively caudad. It is concluded that the younger teeth in each specimen (i.e. partially erupted) developed under the influence of a different gradient than the older teeth in the same specimen. It is concluded that this could account for the difference in crown structure between old and new postcanines. It could also account for the fact that teeth developed at the same time would have had the same basic crown structure.

5. Tooth replacement in gomphodont cynodonts is discussed. It is shown that in *Diademodon* the postcanine row is divided into three regions. The post-canines of the central region always form a structurally graded series. It is shown that during growth teeth were lost anteriorly and added posteriorly; it is shown that the postcanine row continued to be differentiated in the same way despite the posterior migration of the postcanine row during growth. It is concluded that replacement was limited to the anterior and posterior regions and to the anterior and posterior members of the central region. No replacement took place along the remainder of the central region.

It is concluded that during growth teeth were added progressively in *Diademodon* and that large sections of the postcanine row of Diademodon constituted a single *Zahnreihe*. It appears that in this aspect *Diademodon* paralleled later mammals.

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Key to Lettering

a.a.c.	anterior accessory cusp
a.b.	attachment bone
a.c.c.	anterior cingular cusp
a.cing.	anterior portion of lingual cingulum
a.l.c.	anterior labial cusp
a.pc.	additional postcanine
a.l.	alveolus for first postcanine
a.8.	alveolus for 8th postcanine
c.c.	cingular cusp
cing.	cingulum
long.g.	longitudinal groove for the dental lamina
m.c.	main cusp
p.	pit for replacing tooth
p.a.c.	posterior accessory cusp
p.c.c.	posterior cingular cusp
p.c.1.	1st postcanine
p.c.8.	8th postcanine
p.l.c.	posterior labial cusp
p.r.c.	pit containing developing crown of a replacing canine
rep.c.	replacing canine
rep.xi.	replacing incisor
r.pc.	redundant or suppressed postcanine
r.pc.6.	crown of the 6th replacing postcanine